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By Charles T. Brues.

With One Plate.

(Continued from page 3 of cover.)

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OBSERVATIONS ON ANIMAL LIFE IN THE THERMAL WATERS OF YELLOWSTONE PARK, WITH A CONSIDERATION OF THE THERMAL ENVIRONMENT.[1]

By Charles T. Brues.

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The following observations are of a rather fragmentary nature, and their presentation at the present time would demand an apology were it not for the great dearth of knowledge concerning the occurrence, distribution and habits of animal life in the many hot springs and thermal waters so generously scattered over our globe.

A few naturalists have from time to time given their attention to the animal life of certain hot springs, especially in Europe, but the accounts which have been published are so widely scattered that no recent attempt has been made to gather them together for comparison. Nevertheless two zoölogists, Issel ('00, '01, '06, '10) who made extensive studies of the thermal springs of Italy, and Vouk ('19, '23) in Croatia and Slavonia, have indicated several conclusions that may be drawn from a study of the thermal faunæ with which they have dealt. In the present account I have attempted to include a general consideration of the fauna of thermal springs, with particular reference to those groups of animals represented in Yellowstone Park.

My own observations were made during the summer of 1923 when I spent the month of July in Yellowstone Park, devoting a part of the time to a study of the thermal fauna of this exceedingly interesting region. For such a study, the Yellowstone National Park is a particularly favorable field on account of its great extent and the extreme variations presented by the thermal waters, not only in temperature, but in composition and in the ecological conditions which they offer.

For this opportunity to collect material, I feel deeply indebted to Mr. Stephen F. Mather, Director of the National Parks Service who expressed great interest in the biological studies which our party intended to make in the park. The resident naturalist, Dr. Frank E. A. Thone, also received us most cordially and we have him and the superintendent of the Park, Mr. H. M. Albright, to thank for many favors.

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[1] Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 237.

The biological characteristics of thermal waters or "hot springs" depend upon several very evident factors. Of these the most striking is the high temperature of the water. Practically a continuous series with respect to temperature is to be found in Yellowstone Park. From the intermittent geysers water at the boiling temperature is poured forth and certain boiling springs or pools are equally hot at least in the parts where the water is in active ebullition. The outer margins of these pools are cooler and the overflow waters from both geysers and boiling springs gradually cool as they run off in small streams or more rapidly if they spread out over the surface of the soil. From these sources alone there is therefore a complete gradation from boiling water to that which has acquired a temperature as low as that of the surface waters of direct meteoric origin. Other pools and even ponds and small lakes contain water of more uniform temperature far below the boiling point, and often only slightly or imperceptibly warmer than pools or ponds of non-thermal origin. From the standpoint of any aquatic organisms living in such waters, the temperature of the medium is a most important consideration and this is the factor which has most generally attracted the attention of biologists. Before the beginning of the nineteenth century Saussure (1796) noticed in certain European hot springs that there were both plants and animals living in water at temperatures well above those which obtain in places ordinarily populated by living organisms, and since that time it has become more and more clearly apparent that the inhabitants of hot springs are in some way endowed with powers of resistance to heat that is fatal to the ordinary run of animals and plants. The exact nature of the physiological adjustments of this thermal fauna and flora have so far not been satisfactorily determined, although several theories have been advanced to account for the adaptations which undoubtedly exist.

Another common characteristic of thermal waters, particularly of those which emerge from the earth at very high temperatures, is the small amount of dissolved oxygen. As a result of this condition the fauna is further handicapped by the dearth of this essential element, except in the case of certain animals, *e. g.* the adults of aquatic beetles or the larvæ of certain Diptera which secure their oxygen not directly from the water, but from the atmosphere above its surface. This factor is one which has not received sufficient consideration.

Thermal water is also commonly impregnated with salts in solution, and the nature of these is naturally very dissimilar in different places, since it is dependent upon the constitution of the rocks with which the heated water has been in contact. In the Yellowstone Park springs

there are two predominant types, one containing calcium carbonate and the other charged with silica. In the former case the water is acid in reaction due to the presence of much carbon dioxide, and in the latter the silica is dissolved in the presence of sodium carbonate. Other salts that are frequently present are sodium sulphate, sodium chloride and gypsum, with occasionally appreciable amounts of arsenical salts. The addition of such substances to the water is naturally an important environmental factor and presents conditions similar to those existing in alkaline lakes or ponds.

In addition to the carbon dioxide already mentioned hydrogen sulphide is frequently present in considerable quantities, and sulphur dioxide is probably emitted from certain steam vents. I can find no chemical analyses in support of this, but see no other way to account for the presence of charred wood at the openings of many vents. This wood has apparently been acted upon by sulphuric acid derived from the oxidation of sulphur dioxide. In connection with volcanic eruptions, it is of course known that appreciable amounts of sulphuric acid occur in rain water which falls near by.

Occasionally there are also noticeable amounts of finely divided mineral matter in suspension, especially in the tepid pools near the mud geysers or "paint pots."

The ecological peculiarities of the Yellowstone thermal waters are further enhanced by the cold climate of the park which is located near the 45th parallel of latitude. The hot springs are at an altitude of between 6,000 and 7,000 feet which thus places them within the Hudsonian life zone. In the thermal waters and also in the soil immediately surrounding them much higher temperatures of course prevail throughout the year than are normal for this zone and the rigors of the winter are so mitigated that certain animals and plants have found an opportunity greatly to extend their northern range, irrespective of those that seem to be specially adapted to life in or about the hot springs.

As is well known, certain plants occur in water of much higher temperature than that at which any forms of animal life are able to exist. Several botanists (Davis '97, Miss Tilden '98 and Setchell '03) have made observations of the temperatures at which living plants occur in the thermal waters of Yellowstone Park. Of these Setchell's account is the most complete and embodies a long series of observations on springs of different types. He found in the calcareous springs that chlorophyll-bearing algæ occur regularly in water at 60°–63° C. (140°–146° Fahr.) and that forms destitute of chlorophyll extend into still

hotter water of 70°–71° C. (158°–160° Fahr.). These coincide almost exactly with temperatures of 145° and 162° Fahr. observed by us during the past summer and with a maximum of 160° reported years ago by Wood ('68) in Owen's Valley, California. In the alkaline silica-charged waters Setchell found that higher temperatures were compatible with plant life and that species with chlorophyll were growing in water of 75°–77° C. (167°–171° Fahr.) while non-chlorophyll-bearing forms inhabit water as high as 89° C. (194 Fahr.). At the altitude of the Park, the latter is practically the boiling temperature of water.

In the thermal springs of Europe many observations have been made, dating back to those of Saussure, who noted in 1796 the occurrence of plants in the waters at Aix at temperatures of from 35°–46° C. As early as 1854 De Laures ('54–'55) determined that higher algæ ("conferves") grew in the thermal waters of Néris at temperatures of from 42°–48° C. (107°–119° Fahr.) and he further made the interesting observation that the growth of these plants was augmented during the summer, which he interpreted as due to the influence of light over longer daily periods. In Italy Hoppe-Seyler ('75) found at Monte-Grotto near Abano in northeastern Italy algæ growing in water at 50° C. (122° Fahr.) and De Varigny ('93) refers to observations by Martens of Oscillatoria in a hot spring on the island of Lipari at a temperature of 55° C. (131° Fahr.). A slightly higher temperature of 60° C. (140° Fahr.) is reported for Oscillatoria by Schnetzler ('89) at Carlsbad. In the condensed water of steam caves in Ischia Hoppe-Seyler (*loc. cit.*) found green algæ at a temperature of 64.7° C. (149° Fahr.). From these data it would appear that green algæ have been found in Europe at temperatures approximately the same as in Yellowstone Park.

In Iceland several botanists have given accounts of the algæ which occur in the hot springs associated with the well-known Iceland geyser region. West ('02) reports filamentous algæ (Myxophyceæ) in water at 85° C. (185 Fahr.), which is approximately the same as the temperature given by Setchell for Yellowstone Park.

Concerning hot springs in other parts of the world, I have been unable to find many records that seem to be fully trustworthy. In the Himalayas, the eminent botanist Hooker ('54) reported "Leptothrix" in the waters of Thibetan hot springs where the temperature was as high as 75.5 C. (168° Fahr.). Strachey (*teste* De Varigny '93) found living algæ at Pugha in Thibet at 78.8° C. (173° Fahr.) and Dana refers to algæ obtained at 160° Fahr. (72° C.) on the island of

Luzon. In South America Dana speaks of vegetation in the hot springs at Las Trincheras in Venezuela occurring in water as hot as 71° C. (160° Fahr.).

In the Algerian hot springs at Hammam-Meskhoutine, Gervais ('49) found algæ in the second tier of basins of the cascade containing water at 57° C. (135° Fahr.), but the upper layer having a temperature of 63° C. (146° Fahr.) contained none.

Some of these records refer to green algæ, and others like the one at Las Trincheras undoubtedly relate to species without chlorophyll. With this in mind, it is evident that they agree closely with what is known of the algæ and other primitive plants in the thermal waters of Yellowstone Park, with the possible exception that no European species without chlorophyll appear to have been reported from such extremely high temperatures as in other parts of the world.

The temperature requirements for all animals seem to be more exacting than those for the plants just noted, and although I have considered several groups of animals more specifically in the sequel, it seems wise to make a few general statements at this point concerning the reactions of animals to high temperatures and their adaptation to thermal waters.

It is at once evident that practically all groups of animals that are represented at all commonly in fresh water contain a few species known to inhabit thermal waters, and of these a very small proportion seems to be restricted to this habitat. Compared with plants their powers of adjustment to high temperatures are considerably less and even the most resistant forms of animal life are unable to withstand the degree of heat at which certain plants thrive.

From the data furnished by experiments on certain marine animals, it appears very clearly that these forms which have always lived in the sea where they are never called upon to combat great fluctuations in the temperature of the water are far more susceptible to injury from excessive heat. Experiments like those of Richet ('85) and Frenzel ('85) upon a variety of marine animals illustrate this point. The latter author examined a series including a crinoid, actinians, worms, crustaceans, molluscs and a fish (Hippocampus) with respect to the temperatures they could withstand without immediate harm when the medium was slowly heated. In a general way he found that temperatures of from 25°–30° C. (77°–86° Fahr.) were the highest that could be borne even for a few hours, although a mollusc (Murex) (32° C.) and actinians (38° C.) exceeded these figures. According to De Varigny the pelagic *Beroë ovatus* displays a similar critical point of 28°–29° C.

(82°–84° Fahr.) and so far as I can ascertain these figures apply quite closely to all marine metazoa that have been examined. As there are no marine forms occurring in hot springs it is of course impossible to say what their powers of temperature adjustment might be after acclimatization over long periods, but when transferred from a uniformly cool environment it is evident that they are quite susceptible to heat and that forms like the actinian and snail just mentioned which must normally be subjected to excess heat in the littoral of the sea show the greatest resistance. The larvæ of certain marine littoral animals have been examined by Pelseneer ('01) with reference to their resistance to heat and he found that those of certain molluscs, annelids, trematodes and crustaceans were frequently killed by temperatures of 30°–31° C. (86°–88° Fahr.) while others might withstand 37° C. (97° Fahr.). On the other hand he found embryos of the fresh-water *Lymnæa ovata* able to survive a heating of the medium to 44° C. (111° Fahr.).

On account of the great fluctuations of temperature in all except the largest bodies of fresh water, the animals which inhabit them are periodically subjected to considerably higher temperatures than those encountered by marine forms, and we find that the fresh-water fauna is much better able to withstand extremes of heat. Observations cited on a later page by Davenport and Castle and others show that certain amphibians are unharmed by temporary heating of the medium to about 38° C. (102° Fahr.). In thermal springs the tadpoles of certain tailless batrachians have been found living at temperatures noticeably above this and as these are species known normally to inhabit waters of meteoric origin it is evident that they have become acclimatized to these higher temperatures by exposure extending over a number of generations. Fishes are more susceptible to heat, although there is evidence that certain forms have been acclimatized in a similar way. Even fresh-water turtles occur in hot springs according to Schmarda ('53) who cites the finding of these animals in Tunis in springs near the ancient Utica at 44° C. (111° Fahr.) and near Lenkoran on the Caspian Sea in sulphurous springs at 40° C. (104° Fahr.). Among invertebrates the molluscs and insects are most abundantly represented in thermal waters, and, as indicated in detail later, certain members of these groups extend into water of 40° C. (104° Fahr.) and several degrees higher in a few instances.

The range of temperature over which the process of acclimatization may extend is nevertheless very limited and moreover very uniform among quite diverse animals. This is beautifully illustrated by the

classic observations of Plateau ('72) who determined experimentally the thermal death point of a number of fresh-water arthropods known to occur in thermal water as well as in ordinary ponds and streams. When we compare the temperatures at which these animals actually occur in hot springs with the highest temperature that can be successfully endured by unacclimatized individuals of the same species we find that the possible range of acclimatization is remarkably uniform. This is shown in the following table which is based on data furnished by two of the tables given by Plateau.

TABLE SHOWING RANGE OF TEMPERATURE ACCLIMATIZATION.

Species	Highest temperature at which unacclimatized individuals remain alive	Temperature at which individuals have been found in thermal waters	Location of thermal spring
INSECTS			
Culex pipiens (larva)	38° C.	40° C.; 39° C.	Néris; Luxeuil
Cloë diptera (nymph)	44° C. (?)	45°	Luxeuil
Notonecta glauca	37.5°	45°	Vichy
Nepa cinerea	43°	45°	Vichy
Agabus bipustulatus	36°	38°	Ems
Hydroporus dorsalis	39°	42°	Loèche-les-Bains
Hydaticus transversalis	38°	39; 39.2°	Luxeuil; Ems
Hydrous caraboides	38°	40°	Néris
ARACHNIDS			
Argyroneta aquatica	37°	38°	Ems
Hydrachma cruenta	44.5°	46°	Luxeuil
CRUSTACEANS			
Asellus aquaticus	38°	42.5°	Loèche-les-Bains
Gammarus roeselii	33°	34.4; 36°	Piemont; Gastein
Daphnia sima	32.5°	25°	Luxeuil
Cypris fuscata	35°	34.4; 36°	Piemont; Gastein
Cyclops quadricornis	35°	34.4; 36°	Piemont; Gastein

Practically all of the species listed above show that there has been an adjustment which enables them to live continuously at temperatures higher than those at which they are able to remain alive for more than a few minutes when taken directly from fresh water at ordinary temperature. The differences amount, however, to only a few degrees

in each case and we may conclude that the range of temperature adjustment is ordinarily only from one to several degrees Centigrade.

The Protozoa are the most resistant of all animals and Issel ('00–'01) reports Rhizopods and flagellates from hot springs in Italy at 54.5° C. and 51° C. (130° and 124° Fahr.) respectively. Later (Issel '10) he found an Amoeba, apparently the common *A. limax,* in water at 50°–52° C. (122°–126° Fahr.). The same observer found ciliate infusorians extending into water at 46° C. (115° Fahr.). The last is, however, no higher than the temperature for small rotifers and for at least one species of beetles.

The exact relations of terrestrial and aerial animals toward the temperature of the soil and air about them are much more difficult to determine than is the case with aquatic forms. Several reasons for this are self-evident. The specific heat of water is much greater than that of air and soil and the closeness of contact with the soil is so much less than in the case of water that the body heat of cold-blooded animals responds far more quickly and accords very closely with that of the water. The cooling effect of evaporation can also greatly reduce the body heat of non-aquatic animals. Finally, the vast differences between sunlight and shade temperature are in turn modified by the external color of the animals themselves. With such a mass of variable factors, coupled with the fact that most animals may seek the sun or shade at pleasure and may choose between a period of diurnal or one of nocturnal activity, the actual temperatures to which such animals are subjected and the periods of time involved are to be determined only approximately.

In nature the most obvious field for comparison with the aquatic thermal environment is the desert. Desert animals are at times subjected to high temperatures which are quite comparable to those encountered by the inhabitants of hot springs. Here the most important difference lies in the opportunities enjoyed by the members of the desert fauna to escape the excessive heat (and also the dryness) of the surface of the soil by burrowing beneath it during the warmer parts of the day. According to Buxton ('23) the surface temperature of the soil of the desert may normally reach 50°–60° C. (122°–140° Fahr.) in parts of Palestine, while even higher readings of 78°–84° C. (173°–184° Fahr.) have been obtained in other desert regions. The same author records the occurrence of certain insects, two species of Mantis nymphs and adult grasshoppers, actively moving about on the ground where the superficial temperature had reached 50.8° C. (121° Fahr.). Still more recently Buxton ('24) has actually taken the

bodily temperatures of certain desert insects by means of a minute thermocouple which can be inserted *per rectum* into the body of the insect. By this ingenious device he has been able to determine that the body temperature may approach closely to that of the heated soil, but that it always appears to remain slightly lower. Thus in the black tenebrionid beetle, *Ademsia ulcerosa*, body temperatures of from 36°–39.5° were found where the substratum registered 38°–44° C. and in several pale-colored insects the body was somewhat cooler in proportion, registering 33.5°–39.5° when the surface of the soil was 39.5°–45° C. As the opportunities for bodily temperature reduction through evaporation in such chitin-encased animals, possessed of no special regulatory apparatus for this purpose and lacking a readily available supply of water, must always be very scant, the conclusion appears inevitable that the temperature of their bodies cannot regularly be far below that of the soil-surface. Such being the case, it is evident that the temperatures tolerated by desert insects correspond closely to those endured by the inhabitants of thermal waters.

Under experimental conditions the discordant effects of certain factors may be eliminated and this has been done to some extent by several entomologists who have determined the reactions to excess heat and the thermal death point of certain unacclimatized insects. Many years ago Cantoni ('72) examined the behavior of the domesticated silk-worm at abnormally high temperatures and found that they would continue to feed at 47° C. (117° Fahr.). Various others (*v.* Bachmetjew '01) have performed similar experiments with many other caterpillars and found that temperatures of 40°–50° C. (104°–113° Fahr.) are not fatal over periods of many hours. More recently Dewitz ('06) obtained similar results with another series of caterpillars and the larvæ of muscid flies, which place the upper limits of temperature tolerance at 40°–41° C. (104°–106° Fahr.).

In connection with his studies upon the symbiotic intestinal protozoan parasites of termites, Cleveland ('23, '24) has examined with great care the reactions of both termites and protozoa to high temperatures. He found that the thermal death point of the intestinal protozoa is 36° C. (97° Fahr.) while that of practically all of the species of termites with which he worked was considerably higher. The host termites were entirely unaffected by a 24-hour exposure to 36° C. and were able to withstand without injury exposures of ten minutes to 42°–47° C. (108°–117° Fahr.). He thus regards 48° C. as the thermal death point of the termites, although with longer exposures this would no doubt be lowered to some extent.

The very general agreement of nearly all of the observations relating to the fauna of thermal springs with experimental data secured from other animals of the most diverse sorts shows that the tolerance of all animals to high temperatures coincides within quite narrow limits. These would appear to range between 40° and 45° C., or 104°–113° Fahr., usually nearer the lower figure, except in the case of marine species to which as already stated temperatures above 25°–30° C. (77°–86° Fahr.) quickly lead to death. There is also a close agreement between the limits above indicated for non-marine animals and the body temperatures of warm-blooded animals. As the latter are equipped with a thermoregulatory mechanism and are of course not subject to the fluctuations of the medium in which they live we must look for abnormal conditions to determine the upper limits of body temperature compatible with continued life. Such conditions are furnished by individuals, including those of our own species suffering from acute febrile diseases, where the failure of the regulatory apparatus allows the body temperature to rise. Under such conditions a rise of body temperature of a few degrees above the normal level of 37°–42° C. (99°–108° Fahr.) is fatal to the animal. This is in close agreement with the reactions of the lower animals toward heat, especially when we consider that the homoiothermal animal must be regarded as acclimatized to high temperature; or in other words that the warm-blooded vertebrate normally maintains a body temperature very close to the thermal death point.

This uniformity of reaction among the most diverse animals would seem to be due to the fact that high temperatures act directly upon their protoplasm, or at least upon cell metabolism, and this view finds support in the experiments of Vernon ('99) who found in a series of both vertebrates and invertebrates that the voluntary muscles pass into a condition of rigor at temperatures approximating the lethal temperature limit. Unfortunately no satisfactory understanding seems to have been reached concerning the physiology of this process, for upon it must depend any theories relating to the acclimatization of animals to high temperatures. Maurel and LaGriffe ('99) have discussed the matter, but reached no definite conclusions. Davenport and Castle ('95) advanced the theory that the increased resistance of organisms acclimatized to heat is due to a partial dehydration of the protoplasm whereby, on a purely physical basis, its coagulation point is raised in the temperature scale. This theory is based in part on the well-known fact that egg albumen coagulates at higher temperatures as its water content is reduced, and in part on the resistance of

the spores of various microörganisms to temperatures far above those that can be withstood by their actively growing stages. That the same condition holds true in the encysted or desiccated infusoria and even in minute metazoa like the rotifers and tardigrades is also apparently well authenticated. In these animals the amount of exsiccation possible without loss of vitality is surprisingly large. Even in amphibians, *e. g.* Rana, it may proceed to a point where as much as 41% of the body weight may be lost (Hall '22) and subsequently regained without ill effects. In certain batrachians like the desert frogs of Australia such an occurrence normally follows the periodic changes of the seasons. Setchell ('03) from his study of the thermal flora is not inclined to accept this view of exsiccation, at least in regard to the thermal algæ. Applied to the thermal fauna this theory would imply a decreased water content in the blood and tissues and it seems probable that their saline content in most invertebrates is actually greater, due to the excess of salts in the medium which pass into the blood and tissues (Fredericq '04). There is the further evidence (referred to on a later page) that those animals which are able to adjust themselves to the highly saline water of brackish ponds or of the ocean itself are the types which most generally occur in thermal waters.

This question therefore involves physicochemical matters which I do not feel competent to discuss further than to consider the relationships between the thermal and brackish water faunæ. The similarity between these two faunæ and that of the littoral zone of the sea also is very striking and cannot fail to attract the attention of any zoölogist who cares to examine the thermal fauna in any detail. It is frequently referred to in the sequel in connection with various groups of animals, particularly the insects and molluscs. It may be said that a great majority of the animals which occur in thermal waters have close relatives which live in alkaline, saline or brackish water or even in the sea. As the only similarity between all such situations lies in the considerable amounts of soluble salts in the water, irrespective of their nature, it seems reasonably evident that the fresh-water groups of animals that have developed species adapted to thermal waters have done so through their ability to adjust their metabolism to the increased osmotic pressure of the medium. That the members of a number of small quite unrelated groups possess this ability to an unusual extent is equally evident. That much variation occurs among animals in this respect is of course well known (*cf. e. g.* Garrey '05, Sumner '06) and the cases cited indicate that it is not safe to

draw broad conclusions regarding extensive groups of animals from experiments with members of isolated genera or families.

In practically all thermal waters there is undoubtedly a considerable deficiency in dissolved air and a dearth of oxygen compared with meteoric waters as gases are naturally in great part expelled from the highly heated waters when not under pressure. Thus in the overflow from geysers and in pools rapidly supplied by water from boiling springs the process of cooling to temperatures compatible with animal life takes place quickly and there is little opportunity for atmospheric air to be absorbed. The green thermal algæ growing in such water are a source of oxygen supply but the amounts which they are able to furnish to rapidly moving water must be slight even where they are present in a considerable quantity. In the hottest water the non-chlorophyll-bearing plants (*e. g.* Beggiatoa) of course furnish no oxygen and their occurrence indicates the presence of some oxygen in the water when it reaches them.

As already mentioned, many of the animals, *e. g.* many insects and snails, are not entirely dependent upon the dissolved oxygen as they obtain atmospheric air. Nevertheless some are entirely dependent upon what they extract directly from the water, *e. g.* Gammarus and the larvæ of Chironomus and water-beetles. In reference to the fauna of fresh-water lakes, it has been conclusively shown that the amount of dissolved oxygen which varies at different depths is an important factor in determining the distribution of fishes and certain water-breathing invertebrates (Juday '09, Juday and Wagner '09). It is interesting to note that at least one type which Juday found to be characteristic of the lower water layers of Wisconsin lakes occurs in what appears to be one of the most anaërobic situations where I found living animals in the thermal waters of Yellowstone Park. These are the larvæ of Chironomus containing a red hæmoglobin pigment, discussed in the latter part of the present paper.

The thermal fauna has, as we have already stated, undoubtedly been derived mainly from an assemblage of fresh-water animals that have found a suitable if not ideal environment in more or less saline waters of abnormally high and uniform temperature. We cannot, however, consider it at all homogeneous either in origin or in constitution. On the basis of our conception of the geological development of the earth we have only to go far enough back in the evolution of life to reach the point when all animals and plants belonged to a "thermal fauna." Just how elaborate and highly differentiated living organisms may have been at the time when all water on the

earth was at a considerably higher temperature than at present is by no means to be stated. Our knowledge of fossil animals does not however suggest in any way that highly evolved types were present at that time and certainly no one would entertain for a moment the idea that arthropods or molluscs were then in existence. Even if other evidence did not preclude such a possibility it would therefore be fallacious to trace any great part of the present thermal fauna to a primordial one. Schnetzler ('89) would trace some of the highly adapted lower plants like Oscillaria and certain diatoms to a primordial flora, an assumption which is more plausible.

There is no doubt, however, that thermal springs like those now extant have existed in the past as there remain widespread evidences of their activity. It is well known that many fossil plants owe their preservation to the deposition within their tissues of silica derived from hot waters charged with silica in which they have been immersed or from which they may have imbibed the solution by capillary attraction. The "fossil forests" of tree stumps, logs and bits of wood have originated in this way, and in one instance at least it is evident that deposits of fossil insects are to be attributed to the same source (Cockerell '15). In the Gurnet Bay deposit, on the Isle of Wight, there is an accumulation of this sort which includes many insects in addition to numerous molluscs. Concerning the remarkable preservation of the insects Cockerell (*loc. cit.*) says: "There was absolutely no compression, and when the rock is fractured so as to bisect an insect longitudinally, a cast of its internal organs is preserved without losing their more delicate parts as is shown by a mosquito wing still carrying the scales. . . . There was perhaps a mud spring, with heated waters, into which the insects fell, overcome by gaseous emanations."

This Gurnet Bay formation is early Tertiary, probably lower Oligocene, and in connection with the present-day fauna of thermal springs it is interesting to compare the forms which have been found there. Thus, in his account of the insects, Cockerell finds two species of Ephydra and Stratiomyia, both of them genera known to contain modern species that breed in thermal as well as saline waters. In addition there are winged ants and other Hymenoptera, quite similar to the miscellaneous assortment of insects that fall into hot springs. Certain deposits of silicified wood are much older and the preservation of some Cretaceous and even Jurassic wood is so similar to that now in process of silicification that there can be little doubt that the hot springs which furnished the silica were so like those of the present day that they offered similar opportunities for animal life.

On the basis of these facts it may be stated that very probably there have always been hot springs and that they have presented quite similar conditions for a long time, but that their fauna has had its origin in animals from cool fresh water that have become adapted to life in the higher temperatures of thermal springs.

The present-day thermal fauna has been represented by Issel ('06) as composed of several series of animals which he groups as follows:

1. Animals derived from cold water, usually species which are much more abundant and widespread in various other environments and consequently with a greater ability to accustom themselves to extreme conditions (*e. g. Philodina roseola, Chilodon cucullus*).
2. Animals that come periodically from the sea (*e. g. Anguilla vulgaris*), or which migrate for short periods into fresh water from the sea (*e. g. Palaemonetes varians*).
3. Animals that although absent in the ordinary waters of the region, occur in that of warmer regions (*e. g. Hydroscapha gyrinoides*).
4. Animals at present restricted to the thermal waters of a region, but similar to fossil species of wider distribution in deposits from ordinary water in the same region (*e. g. Melanopsis etrusca*).
5. Animals up to the present time apparently restricted to thermal waters (*e. g. Laccobius sellæ*).

Quite recently Vouk ('23) has grouped the thermal fauna and flora on the basis of the temperature of the water and indicates three divisions as follows:

1. Hypothermophilous Formations, below 15° C. (58° Fahr.).
2. Mesothermophilous Formations, 15°–30° C. (58°–86° Fahr.).
3. Euthermophilous Formations, 30°–80° C. (86°–176° Fahr.).

This classification is essentially arbitrary and artificial as it fails to recognize the varying critical temperatures for different types of organisms, although in its gradually rising scale, it necessarily reflects to some extent the progress of adaptation. From what has already been said concerning the temperatures withstood by unacclimatized animals of most kinds it is evident that there is a clearly marked point in the neighborhood of 40° C. (104° Fahr.) which is highly significant, as it is the upper limit for all but the most resistant animals. Among plants on the other hand, as already mentioned, temperatures in the neighborhood of 60° C. (140° Fahr.) are critical as they mark the upper limits for chlorophyll-bearing vegetation.

Issel's classification is based on the probable evolutionary development of thermophily. The most recent accessions to the fauna are

placed in the first category and those types which are undoubtedly the oldest are placed last, and the arrangement thus conforms to the probable origin and development of the thermal fauna as we have outlined them above. Applied to Yellowstone Park, all of the above categories are included, with the exception of the second which is precluded by the topography of the region, and the fourth for which I cannot at present pick out any well-authenticated case.

The first group is typified by a widespread species like *Gammarus limnæus;* the third by *Libellula saturata* and *Tropisternus californicus;* and the fifth by *Ambrysus heidemanni* and the Chironomus larva (sp. near *tentans* described in the sequel).

The remainder of the present paper contains a more detailed account of the findings in Yellowstone Park and in connection with these I have attempted to summarize the present knowledge relating to the occurrence in thermal waters of each group that is referred to. As has been mentioned at the outset, the literature is widely scattered and many references to the thermal fauna, or ones important in connection with it, are included in works not dealing primarily with this subject. For this reason, a bibliography has been appended which includes the titles to which specific reference is made in the text.

INSECTS.

Order Diptera.

Family CHIRONOMIDÆ.

The larvæ of three species of this family were found in the thermal waters of the Park, one of these in quite hot water, the others in streams and pools where the water was only slightly warm, although of thermal origin. Adults were not reared, but as the early stages of this family have been so extensively studied it is possible to classify their larvæ with considerable accuracy.

Chironomid larvæ, usually "blood-worms" of the genus Chironomus, have been mentioned a number of times as inhabitants of thermal and alkaline waters and a number of genera are known to be either exclusively marine or to include marine species. Wood ('68) seems to have been the first to record the presence of Chironomus larvæ in hot springs; these were observed by one of his correspondents in Owen's Valley, California, who found them in water said to be at a tempera-

ture of 51° C. (124° Fahr.). Hubbard ('92) speaks of the larvæ of minute gnats in the tepid water of the terrace basins at Mammoth Hot Springs in Yellowstone Park and these undoubtedly were Chironomidæ. Schwarz ('14) found the larvæ of two minute species of Chironomidae in water between 38°–40° C. (100° and 105° Fahr.) at Hot Springs, Yavapai County, Arizona. Issel ('01) found Chironomus in one of the Italian hot springs at 36° C. (97° Fahr.).

Ceratopogon may also be represented in alkaline ponds by a species from the western states. Packard ('71) described a supposed Tanypus from Clear Lake, California, which Johannsen has been able to refer to Ceratopogon *sens. lat.* As these specimens were really from an alkaline pond in the vicinity of the fresh-water Clear Lake (Packard '83), it seems evident that at least one species of this highly polymorphic and widely distributed genus breeds in alkaline water. Larvæ of Culicoides were found by Ping ('21) in artificial saline pools near Ithaca, New York, having a slight salinity. The two closely related genera Eretmoptera Kellogg ('00) from California and Psamathiomyia Deby ('89) from western Europe are both maritime, their larvæ living in tide pools in the American form and on alga-covered rocks in the case of the European one which feeds on Enteromorpha. Both have vestigial wings in both sexes.

Thalassomyia frauenfeldi Schiner of northern Europe is also marine. The larvæ have been found several times along the coast of England by Swainson (Theobald '92) attached to hydroids, and also among seaweed. On account of its unusual habitat it was mistaken for an annelid-worm by Johnston, who described it as *Campontia eruciformis.* Johannsen ('05) believed that Thalassomyia might be synonymous with Scopelodromus, but if the published figures are accurate it is evident that the larvæ, at least, differ considerably, as those of the former are represented as having four pairs of ventral blood-gills while those of the latter have none.

In Scopelodromus Chevrel ('03), represented by a single species, *S. isemerinus,* the larva is marine also, the types coming from seaweed collected on the coast of France. As mentioned above, this may be a synonym of Thalassomyia.

Still a third similar genus, Halirytis, from the remote antarctic, is known from Kerguelen Island. The type *H. amphibius* Eaton ('75), also figured by Verrall ('79), is also subapterous at least in the female which occurs along the shore where the larvæ probably feed on Enteromorpha. Another antarctic genus from Patagonia, Bergica Jacobs ('00), has greatly reduced wings in both sexes and the larvæ are probably marine also.

The European *Clunio marinus* Haliday is well known as a maritime midge, with a marine larva obtained by Carpenter ('94) who has made interesting observations on the habits of the species. The female only, in this case, is unable to fly and is carried about by the male.

Species of Chironomus (*sens. str.*) are also known to be truly marine, *e. g. C. thalassophilus*, bred and studied by Bequaert and Goetghebuer ('13) in Belgium, and an unidentified species found in salt water on the coast of France by Moniez ('90). Larvæ of an unidentified species were even found in the pools of slightly saline water near a salt works at Ithaca, New York, by Ping ('21).

In eastern North America several marine larvæ have been found, but they have never been adequately described and their identity is unfortunately more or less shrouded in mystery. The first references are by Packard in 1869 ('69a, '69b) and relate to the larva of *Chironomus oceanicus* Pack., placed with some doubt in the genus Orthocladius by Johannsen ('05). *C. oceanicus* was found in several localities on the Massachusetts coast.

From the preceding account, it is evident that many members of this family in the most diverse parts of the world show adaptations to life in thermal waters, alkaline ponds and to marine life in the littoral zone.

A more specific account of my own collections in Yellowstone Park follows.

Chironomus sp., near *tentans* Fabr.

(Fig. **1**, Fig. **2**, *a.*)

The peculiar larvæ of this species were taken in a warm pool about two miles east of the point where the Yellowstone River emerges from Yellowstone Lake. Near this point there is a small number of hot and warm pools and a few steam vents within several hundred feet of the lake shore, but separated from it by an irregular, low-lying ridge a few feet in height. One more or less circular pool, about fifty feet in diameter, bore bird-tracks in the soft ooze within a few feet of its border, beneath a layer of water several inches in depth, and numerous bright red larvæ were readily to be seen in the water at a temperature of about 49° C. (120° Fahr.). As the zone in which they occurred was of considerable width there was a corresponding variation in temperature but some larvæ at least were in water of this temperature.

These larvæ undoubtedly belong to some rather large species of Chironomus, and as they are strikingly different from those of any species so far described I have thought it worth while to describe and figure them.

The larvæ measure 9–11 mm. in length; of the usual slender form prevailing in the genus; bright red in life, white as preserved; head capsule light testaceous, darker on the sides, with the posterior margin black ventrally and laterally; teeth of mentum, tips of mandibles and hooks of anal prolegs black; bristles on prothoracic prolegs brownish yellow. Two eye-spots on each side, of about equal size, separated by about twice their own diameter. Long joint of antenna cylindrical, three times as long as thick; second joint small, as long as the width of the first and of about the same shape, bearing internally at the base

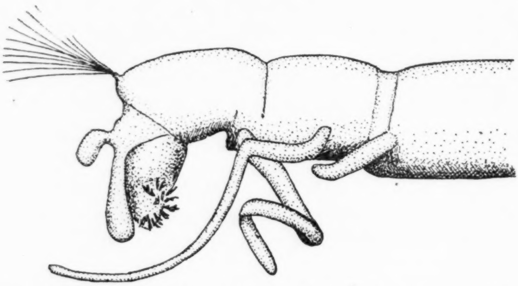

FIGURE 1. Chironomus sp., near *tentans* Fabr. Posterior part of abdomen of larva in lateral view.

a stout bristle somewhat longer than the joint; third joint minute, globose; fourth a minute cylinder with a short apical appendage. Mentum (Fig. 2, *a*) broad, with its dentate edge evenly curved; median tooth broad, but not very long; first lateral short, acute; second the longest, rather closely united to the third; teeth to the last (sixth) decreasing in size from the second lateral. Mandible with three strong teeth before apex, with a series of conspicuous hairs inwardly that reach beyond the tip of the mandible; apex bidentate, the upper tooth brown and shorter than the ventral black one; outer side with a bristle externally near the base. Prothoracic prolegs extending as far forward as the eyes; their tips clothed with simple, strongly curved bristles. Posterior part of body (Fig. 1) bearing three pairs of ventral blood-gills, a pair attached near the ventral lateral angles of the seventh segment, as long as the thickness of the body; a second pair laterally at the middle of the eighth segment, these long and sharply geniculate near the base; a third pair near the anterior ventral angles of the ninth segment, these spirally curled; tenth abdominal segment

with two dorsal pairs of blood-gills, the apical pair longest. Ninth segment dorsally at apex with a pair of median approximate nipple-shaped processes bearing together a cluster of about ten long bristles. Anal prolegs tipped with a crescent-shaped group of about a dozen bifid and trifid hooks.

This larva is remarkable in having three pairs of ventral abdominal gills. There are a few species known to have one or two pairs, but

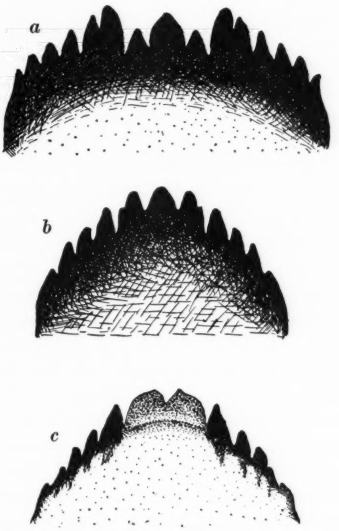

FIGURE 2. *a*, mentum of Chironomus sp., near *tentans* Fabr.; *b*, mentum of Chironomus sp., near *tenellus* Zett.; *c*, mentum of Orthocladius ? sp.

so far as I can ascertain positively, this is the first one to have a pair on the ninth segment. Whether this extra pair bears any relation to the undoubtedly low content of oxygen in the water which it inhabits, it is impossible to say, but this may quite possibly be the case. The supposed annelid, *Campontia eruciformis* (Johnston '65, Verrall '79, Theobald '92), which, as already mentioned, is probably the larva of Thalassomyia, appears to bear four pairs of ventral gills near the posterior part of the body, but the figure is so diagrammatic that this is open to question. The checkered taxonomic career of this

species and the dissensions which it caused are also related by Pavesi ('81). In structure the present larva agrees with those figured by Weyenbergh ('74), Johannsen ('05) and Malloch ('15) as *Chironomus tentans* Fabr. in the form of the mentum and mandibles, and were it not for the three pairs of gills, it might perhaps be considered as this species, although very similar to *C. viridicollis* V. d. Wulp, and to *C. decorus* Johannsen. Weyenbergh's figure (*loc. cit.*) does not show the gills.

Chironomus sp., near *tenellus* Zett.

Length 6 mm. Color as preserved in alcohol distinctly banded, the intersegmental bands pale, but each body segment brownish due to a very fine shagreen-like speckling of pigment. Head capsule very dark piceous, almost black; a pair of eye-spots at each side of the front, the anterior one only half as large as the posterior and separated from the latter by less than its own diameter. First joint of antenna long, cylindrical, three times as long as thick; second minute, but little longer than wide, as long as the width of the first; fourth and fifth barely visible, the terminal appendage obsolete; bristle-like appendage at base of second joint apparently not present. Mandible with three long teeth before apex and trace of a fourth basal to the others; its outer edge fluted (*i. e.* with a series of emarginations) and bearing a large bristle near base and another before the middle; inner surface without a tuft of hairs. Mentum (Fig. 2, *b*) narrow, the anterior margin strongly arched, deeply pigmented except for a hyaline setigerous spot near each hind angle; median tooth large, rounded at tip; first lateral tooth united with the second which shows only as a notch on its exterior side; third separated by a deep cleft; fourth to sixth decreasing in size. Prothoracic prolegs slender; their apical pads distinctly separated, clothed with dense brown curved bristles. Apical abdominal segments without ventral blood-gills and the two pairs of dorsal ones on the last segment extremely minute. Anal prolegs long and slender, their tips armed with the usual bifid hooks. Eighth abdominal segment with a pair of minute bristles near the middle on the ventral surface; tenth with a similar pair, one at the base of each proleg and above with a pair near the base of the blood-gills; ninth segment with a pair of approximate nipple-shaped tubercles bearing long hairs.

This species was taken together with the larvæ of Tabanus and dragon-fly nymphs mentioned on another page in an inactive pool of very turbid water at West Thumb. The temperature of this water

is only slightly elevated and it is well aerated, due to the presence of growing Chara-like plants in abundance.

This larva resembles closely that of *Chironomus tenellus* Zett. as described and figured by Johannsen ('05) and may be that species.

Orthocladius? sp.

Length 8 mm. Color as preserved pure white, the head capsule pale luteous, with only the tips of mandibles, anterior margin of mentum and eye-spots black; bristles and hooks on prolegs pale brown. Antenna with first joint more than three times as long as broad and slightly tapered to the tip; second joint twice as thick and as long as the thickness of the first joint; third and fourth joints minute, apical appendage barely visible; second joint without secondary, ramus-like appendage. Mandible with four distinct, but rather short preapical teeth; outer edge smooth, with a very delicate hair before the middle; inner surface without hair-tuft. Mentum strongly arched along its anterior margin; no median tooth, but the middle pair large and broad (Fig. 2, *c*) and weakly pigmented; in addition to these there are five lateral teeth, gradually decreasing in size, the notches between them distinct, but not very deep. Lateral eye-spots very close together, the posterior one more than twice as long as the anterior. Prothoracic prolegs very small, but with their tips separated; apical pads clothed with extremely short, sharply curved bristles. Anal prolegs long and slender, tipped with pale brown bifid hooks. No ventral anal gills. Dorsal ones in two pairs; small, the upper pair somewhat larger than the lower; porrect and extending laterally. No bristles near apex of abdomen except for the two tufts at the apex of the penultimate segment; each consists of seven or eight hairs, twice as long as the diameter of the segment, and placed on a short cylindrical tubercle close to the dorsal median line.

This is probably an Orthocladius, as it agrees most closely with the known larvæ of this genus. It is easily recognizable by the pale, bidentate apex of the mentum. A pale median tooth or teeth seem to be more or less characteristic of Orthocladius, although not entirely restricted to it. Johannsen ('05) mentions (p. 249) a supposed Chironomus larva in which the median pair of labial teeth are paler than the others. It is of interest to note here that the marine Chironomid described many years ago ('69) by Packard as *Chironomus oceanicus* has been doubtfully referred to Orthocladius by Johannsen ('05); this species has been mentioned already on a previous page.

The present larva was collected at West Thumb near the shore of Yellowstone Lake in warm water which flows through coarsely spongiform siliceous deposits below the boiling springs. The temperature of this water was about 100° Fahr.

That the absence of ventral anal gills is not necessarily associated with an abundant supply of oxygen is evident from a note of Malloch's ('14) in which he records the occurrence of the giant blood-worm, *Chironomus ferrugineovittatus* Zett., in mud under 10–12 feet of water. This species has no ventral anal gills.

The presence of hæmoglobin in the larvæ of certain forms was originally interpreted as an adaptation to life under more or less anaërobic conditions by Miall ('91, '95) and this is no doubt true in a general way, although there are chironomid larvæ without this pigment which are able to exist in places where the oxygen supply is scanty and on the other hand true blood-worms often inhabit well-aërated waters. These discrepancies have often received comment (*cf.* also Gahan '12, Malloch '15, Muttkowski '18). The latter observer found some forms, *e. g. C. tentans* Fabr., practically confined to the bottom layer of Lake Mendota, Wisconsin. According to Miall's hypothesis they would have to come nearer to the surface periodically in order to lay up a store of oxygen. Such migration although apparently not regularly observed under such conditions would be obviously of no use in the case of larvæ living like the one described in the mud of shallow hot pools where the oxygen content can be no greater at the surface.

Leitch ('16) has studied experimentally the rôle of hæmoglobin in Chironomus and also in the snail, Planorbis, and comes to the conclusion that the function of hæmoglobin in these two animals, and among those invertebrates in general where it occurs, consists in making available, by its power of binding oxygen chemically, a quantity of oxygen sufficient for the needs of the animal at oxygen tensions so low that the necessary amount is not supplied by physical solution. He has shown also that the actual storage capacity for oxygen of the hæmoglobin in the Chironomus larva is sufficient for only a few minutes of anaërobic life. Thus hæmoglobin is characteristic of many mud-inhabiting invertebrates (Van der Hyde '17) that live where oxygen is present in only very small amounts. On the basis of Leitch's data we may thus interpret the ability of the larvæ of Chironomus to live under more or less completely anaërobic conditions, and we find them in the lower waters of lakes where the presence of oxygen cannot be detected by ordinary means. This is a common occurrence in fresh-

water lakes (*cf.* also Immel '16) and in thermal waters (Ziegelmayer '24). In the alkaline water of silica-bearing hot springs there is the added fact that among fishes at least, an increased alkalinity serves in some way to increase the resistance of these animals to a lack of oxygen (Packard '05) and the same is probably true of Chironomus as the hæmoglobin appears to be identical in the two cases. There is one disturbing fact, however; Ping ('17) found that the larvæ of one species of Chironomus do not become red till they have attained a length of 5 mm. If this holds true for all the species the matter of respiration in these inhabiting thermal springs still remains obscure. It is true that the larvæ of certain related flies of the genus Corethra, (Juday '21) which live in the ooze at the bottom of lakes, do not enter the mud when very young, but this would not explain the case of the Chironomus larvæ in thermal waters even if they have the same habits, for they are confronted by an equally low tension of oxygen during their entire development and they cannot escape it by seeking water at a different level.

Family CULICIDÆ.

Mosquito larvæ were found at only one locality breeding in the truly thermal waters. At West Thumb there are many inactive pools containing water which is only very slightly warm, although giving off gas in small amounts, and opaque from fine clay in suspension. These are really inactive mud volcanoes or "paint pots." In several of these the larvæ of *Culex tarsalis* Coquillett were extremely numerous, together with some small Dytiscid beetles. This species has been reported by Dyar ('23) as breeding in such pools and in the sulphurous marshes of the Park. He found *Culiseta inornata* Williston in similar places, but this species is not represented in the present collections. From their known habits and distribution it is evident that neither of these species is restricted to alkaline or thermal waters.

The larvæ of a rather large number of mosquitoes breed in brackish water or even in water of very high salinity, some regularly and others only occasionally. Howard, Dyar and Knab ('12) refer to three species — *Aëdes zammittii* of the Mediterranean region which breeds in rock pools containing concentrated sea water only; *Aëdes fluviatilis,* and a species of Stegoconops in the American tropics which breed also in the concentrated sea water of rock pools, but in fresh water as well. In the case of some of the many maritime species breeding in brackish water at least, the adjustment of the larvæ to certain concentrations

of sea water is rather delicate, and their distribution is sometimes determined by the amount of salinity. This relation has been examined experimentally by Chidester ('15) who finds that the optimum salinity for the two abundant salt-marsh species (*Aëdes cantator* and *Aëdes sollicitans*) in New Jersey is quite different and also that *Culex pipiens* is unable to withstand salinities approaching those which the former species resist. The same author attempted to determine the relations of the several more abundant salts in sea water to the larvæ, but his results appear to be inconclusive in this respect.

Several species breed more or less regularly in alkaline water in the western states, and in the case of *Aëdes dorsalis* Meigen, a European species common to North America, the larvæ have been found in perfectly fresh water, alkaline pools, salt-marsh pools and even in the vats at salt works. In inland salt pools Ping ('21) finds that this species breeds only in those of low salinity (6% or less). The adults show remarkable variations in color, possibly associated with the different larval habitats. The ability among mosquitoes to breed occasionally in strongly alkaline water is recorded by Ballowe ('18), who found "both Anopheles and Culex" successfully developing in water containing sufficient caustic soda [probably transformed to sodium carbonate after standing for a long time] to give it a strongly alkaline taste. A lesser ability to withstand slightly concentrations of sea water has also been observed many times among a number of Anopheline mosquitoes in various parts of the world (De Vogel '07, Foley and Yvernault '08).

The occurrence of mosquito larvæ in actually thermal water seems to be very unusual, although two particularly interesting observations have come to my notice. Tamayo and Garcia ('06) obtained larvæ of an Anopheles at Lake Huacachina, near the coast in southern Peru. The temperature of this lake is about 75° Fahr. The species, which they named *Anopheles peruvianus*, is according to Knab ('15) the widespread neotropical *A. pseudopunctipennis* Theob. This species extends only sparingly into the warmest parts of the United States, but has been found in water perceptibly warmed by the influx of thermal water at Las Vegas Hot Springs, New Mexico, which is in the Transition Zone (Needham and Cockerell '03).

In Europe the larvæ of the common house mosquito, *Culex pipiens*, have been reported from thermal waters at Néris (40° C.) and again at Luxeuil (39° C.), according to Plateau ('72). Ziegelmayer ('24) found the larvæ of an undetermined mosquito abundant in the Italian sulphur springs known as Aque Albule.

Family STRATIOMYIDÆ.

Larvæ of a species of this family were obtained at only one place, but as their habits serve to conceal them well, I do not doubt that their distribution may be quite extensive about the hot springs in the park.

In the canyon of the Yellowstone, about half a mile below the trail that leads down to the east bank of the river is a small cone-shaped geyser that sprouts more or less continuously to a height of a few inches close to the water's edge. Above it the canyon walls rise precipitately and are covered in streaks with an alga growing in water that trickles over the rock. Well hidden in this growth were numerous Stratiomyiid larvæ along the edges of the flow where the water had cooled sufficiently to feel only warm to the hand. As in the case of all flowing warm water of this type, the course of the flow is continually changing as algæ grow and the mineral deposits form. Consequently the station occupied by these larvæ is not only very limited in extent, but is continually shifting. In consequence they live a rather precarious existence, in danger of dessication if the water is diverted away and liable to still more sudden destruction should the hot water flow over them. The consequence of the latter alternative was seen in a number of larvæ which I recovered from a flow of very hot water several feet away. These had succumbed to the sudden rise in temperature and were already accumulating on the surface of their bodies a mineral deposit, becoming literally fossilized while still entangled in the mass of alga surrounding them. Viewed under the microscope the deposit is seen to consist of minute, nearly spherical bodies, which, as they are readily dissolved by hydrochloric acid, consist of calcium carbonate. They form in an irregular superficial coating and the larvæ are not destined to become recognizable fossils.

Following is a description of the larvæ.

Stratiomyia sp.

(Fig. **3**.)

Length when well extended 23–28 mm.; greatest width about 3 mm. Head very dark above, pale beneath; body more or less distinctly longitudinally vittate above, with a median dark stripe and two on each side, one of which lies close to the lateral margin; apical segment much darker. Eyes placed close to the anterior corners of the head.

Body broadest at the base of the abdomen and more gradually tapering posteriorly than in front. Prothoracic spiracle behind the middle of the lateral margin, circular, with a radially fluted ring; posterior respiratory sac opening by an apical semicircular slit, fringed above and below with a series of plumose hairs, about 12 or 15 in each row. Body conspicuously hairy, but with the base and apex of each segment

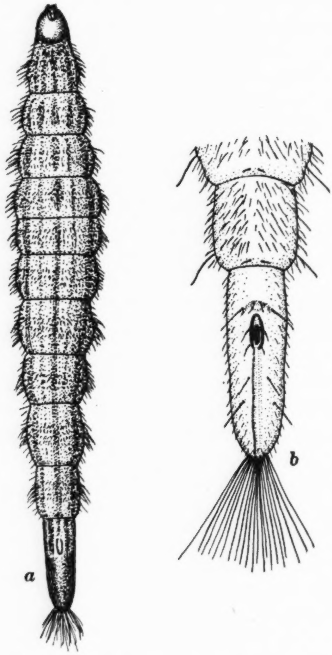

FIGURE 3. Larva of Stratiomyia sp. *a*, dorsal view; *b*, posterior portion in ventral view.

bare. Integument of the usual shagreened structure. Apical segment very slightly more than three times as long as broad and about one-half longer than the penultimate in moderately expanded specimens. Second abdominal segment below without hooks or stout bristles as are all segments except the penultimate which bears a pair of small, almost minute stout bristles behind near the median line;

close examination reveals a similar pair, noticeable only under high magnification, on the antepenultimate segment. Anal slit terminating before the middle of the last segment.

According to the characters given by both Malloch ('17) and Johannsen ('22) these larvæ undoubtedly belong to the genus Stratiomyia and agree quite closely with the larva of *S. discalis* Loew according to Johannsen's key.

I obtained adults of three species of Stratiomyia in the Park where they frequent the flowers of *Heracleum lanatum* in company with many Hymenoptera and other Diptera, but no specimens were taken either by Professor Melander or myself in the neighborhood of the place where the larvæ were found.

The aquatic larvæ of this family are said to feed generally upon algæ and decaying matter, and possibly to some extent upon minute forms of animal life and the present species undoubtedly depends for food upon the algal growth in which it occurs.

The larvæ of the subfamily Stratiomyinæ are all aquatic, occurring in waters charged with lime at least in small quantities and regularly accumulate on the surface of the integument deposits of calcium carbonate from which they must be freed by immersion in dilute hydrochloric acid before they can be satisfactorily studied. Their occurrence in hot springs has been previously noted by Packard ('82) who gave a brief account of some larvæ collected by H. G. Griffith in a hot spring in Gunnison County, Colorado. The water in which they occurred is said to have been at 157° Fahr., but as this is so close to the coagulation point of insect protoplasm and barely below the highest temperature at which the most resistant algæ disappear I am inclined to believe that the larvæ must have been in adjacent water of lower temperature. From Packard's brief description it is probable that these larvæ represent a species of Stratiomyia, as he speaks of the anal segment as tapering and four times as long as broad, while no mention is made of the hooks on the penultimate segment characteristic of Odontomyia.

Another interesting case of the larvæ of some unidentified Stratiomyid is cited by Johnson in his study of this family ('95). The note, published in a newspaper (Evening Call, Lincoln, Neb., April 5, 1895), was written by Professor Lawrence Bruner, and the wording leaves little doubt that it has been printed essentially as written by the well-known entomologist. The specimens came from a thermal spring in Vinta County, near the extreme southwestern corner of Wyoming, collected by Mr. John C. Hamm. Johnson quotes this

article as follows: "At the time I saw the larvæ in their native habitation I did not have a thermometer with which to take the temperature, but the water was so hot where I saw them I could not hold my hand in it. My best judgment is, and was at the time, that the water was not more than twenty or thirty degrees below the boiling point.... In color they are dull gray, in form much flattened, and in size the length of the line below the figure [15 mm.]. The two specimens examined by me are more or less encrusted with sulphur and other mineral substances."

According to this account the temperature of the water would have been 170–180° Fahr., unquestionably an impossible condition. It is of course easy to overestimate the temperature of hot water with the hand which can endure a temperature of about 140° Fahr. only with great discomfort.

In Europe Stratiomyiid larvæ are known from thermal waters. Issel ('00, '01) reports two cases in his paper on Italian hot springs, once at a temperature of 22.5° C. in the vicinity of Tivoli, near Rome, and again from the Valdieri springs in water of 37°–38° C.

Stratiomyid larvæ are known to occur in salt water also. In 1871 Packard reported the occurrence of a species in Clear Lake, California, as he supposed in salt water, but according to Aldrich ('12) this lake is fresh. It appears from a later note of Packard's ('83), however, that these specimens were really from Borax Lake and the species is therefore to be considered as an alkaline water form. Whether it may be a Stratiomyia or an Odontomyia is difficult to determine from the description. A truly marine larva, probably Stratiomyia sp., obtained by A. W. Pearson on the New England coast near the mouth of the Merrimac River is recorded by him ('83). This larva was living in a mass of sea wrack (Zostera).

Similarly, in Europe, larvæ of Stratiomyia have been found to develop in salt water. Florentin ('99) found the larvæ of *S. chameleo* Deg. living in excessively saline water with a salt content of 78 grams to the litre in the salt marshes of Lorraine. In Great Britain, Yerbury ('19) states that *Stratiomyia longicornis* Scop. has been bred from a larva found under rotting seaweed.

Larvæ of the related genus Odontomyia do not occur so generally in alkaline and saline pools, but Mr. C. W. Johnson tells me that he once reared a specimen of *O. cincta* Oliv. from a larva found in a salt marsh.

FAMILY TABANIDÆ.

The larvæ of a large species of Tabanus were found in thermal waters of the Park. Unfortunately the adults could not be bred out, and they belong to a species hitherto undescribed in the larval stage. Adults of at least six species of Tabanus were collected during our stay; the most abundant one, *T. osburni* Hine bothered us very frequently; the others (*T. affinis* Kirby, *T. phænops* O. S., *T. opacus* Coq., and *T. septentrionalis* Lw. and *T. punctifer* O. S.) were much less numerous, and all with the exception of *T. punctifer* are too small to associate with the larvæ collected. It is possible that adults of the latter were not flying at the time of our visit, or the larvæ may be those of *punctifer*, although this species has been rarely taken in localities that are far from thermal or alkaline waters.

A description of the larva follows.

Tabanus sp., probably *T. punctifer* O. S.[2]

(Fig. **4**.)

Length in moderately extended condition 30–35 mm. Of the Of the usual pale buff or whitish color with dark brown markings as follows: stripes along median ventral and along each of the later prothoracic grooves; anterior margin of mesothorax, broader laterally above, narrowed medially above and obsolete below; the four lateral stripes extending nearly to the posterior margin of the segment and broadened apically; metathorax similarly marked, except that the band is not narrowed above nor below and the lateral stripes are much attenuated behind; abdominal annuli similar on the seven basal segments, each formed of a basal band, paler below and broken above by a white transverse band about half the width of the segment and one-third the width of the annuli; seventh abdominal segment also with a narrow longitudinal stripe along the lateral line; eighth with a similar broader one, as well as its complete apical margin and a curved band encircling the anal tubercle behind. Prothoracic spiracle, mandibles and posterior spiracle piceous or black. Mandibles with the inner edge very finely serrate, the teeth directed slightly backwards toward the base of the mandible. Second joint of antenna terminating in a short seta, very much more slender and about half as long as the first, articulated in an emargination before the apex of the first. Palpi three jointed, joints of about equal length, but the second and

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[2] See postscript on page 424.

third respectively are much more slender. Lateral striated area of prothorax extending over only its posterior third; the dorsal and ventral surfaces smooth except for a few very fine striæ on posterior fourth. Lateral areas of meso- and metathorax strongly striated between the longitudinal brown bands, the striæ extending from the basal anterior brown band almost to the posterior margin; upper and lower surface of mesothorax smooth, with a few weak striæ behind across the middle portion; metathorax, both above and below, finely

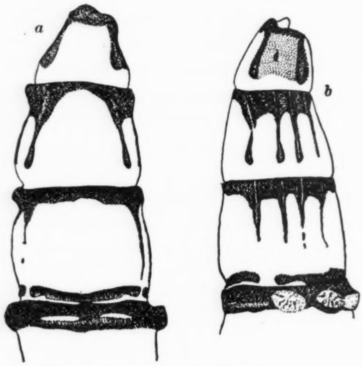

FIGURE 4. Larva of Tabanus sp., probably *T. punctifer* O. S. *a*, anterior part of body in dorsal view; *b*, same in lateral view.

reticulate striate, with an area at each side near the base, more nearly smooth. Pale parts of abdomen striate, more densely so on the sides and more sparsely so above and below where the surface is sometimes more or less reticulate. Body setæ few, very short and inconspicuous; each thoracic segment with a short bristle near the middle of each side of the ventral area; apex of abdomen with three pairs of very small ones along the sides of the spiracular opening.

The larvæ of this species were found in moderately warm water; in Bath Lake (33° C.; 91° Fahr.) July 7 and also in a small warm pool of about the same temperature at West Thumb on July 16. Another collection from the stream which serves as an outlet to Firehole Lake contains small larva which probably belongs to the same species; this water is also warm, about the same temperature at this point as at the other two stations, and very heavily charged with silica in solution.

These larvæ fall in the group with *Tabanus atratus* Fabr. as characterized by Hart ('95) on account of the reduced size of the lateral striate areas on the prothorax and the well-developed lateral longitudinal bands on all the thoracic segments.

I can find no records of the occurrence of larvæ of Tabanus in hot or warm springs, nor in alkaline waters. One European species, *T. autumnalis* L. has once been found in the salt lakes of Siebenbürgen (Friedenfels '80), and although no larvæ of the common "green-head" *T. nigrovittatus* Macq.) of the eastern Atlantic seaboard appear to have ever been taken, there can be little doubt that this species develops in the salt marshes along the coast. Schwarz ('91) in his account of the insects of Great Salt Lake, Utah, mentions the occurrence of larvæ of one or several species of Tabanus in the salt flats where the water of the shallow pools is more or less mixed with fresh or sulphurous water.

Johnson ('19) mentions the occurrence of two varieties of the common American *Tabanus atratus* Fabr. along the Atlantic coast, var. *nantuckensis* Hine in New England and var. *fulvopilosus* Johnson from New Jersey to Florida. These forms are so strictly confined to the marshy coast that he is convinced that they breed in the salt marshes. In this case, it is evident, as with the mosquitoes mentioned above, that the salinity of the breeding grounds is associated with discernible morphological characters in the adult flies.

No larvæ of Chrysops were found in any of the thermal waters, but several species were very annoying in the Park, usually in the woods. One species, however, never appeared in such situations, but was almost invariably noticed when we collected in the vicinity of the thermal pools. This is *Chrysops fulvaster* O. S., a form rather widely distributed in this region, and I think very probably associated with alkaline water and hot springs. Aldrich ('13) mentions its occurrence on the shores of Box Elder Lake, a brackish pond at Brigham City, Utah. Along the eastern coast of North America it is probable that *C. fuliginosus* Wied. (*plangens* Wied.) is restricted to the salt marshes (Johnson '19).

Family EPHYDRIDÆ.

So far as their adaptations to alkaline and saline water are concerned, the larvæ of this family are perhaps the most remarkable of the order Diptera.

Both in Europe and in North America, several species of the genus

Ephydra have long been known to inhabit salt pools along the seacoast, as well as inland salt and alkaline lakes, and even the concentration vats of salt works. Nearly a century ago *Halmopota salinarum* was found by Bouché ('34) in brine pits, and a few years later the common European *Ephydra riparia* was found by von Heyden ('43–'44) to breed in similar situations. Later a number of other species of Ephydra, Dimeacenia, Cænia, Pelina and Parydra have been added to the list. In America the larva of Ephydra was first described by Packard ('69a, '69b, '71) from tidal pools on the New England coast, Great Salt Lake, Utah, and Borax Lake, California. Various other entomologists later interested themselves in these strange larvæ, but it remained for Aldrich ('12) to examine more closely into the habits and distribution of several of the species that occur in the salt and alkaline lakes and sea coast of the western United States. Their great abundance in Great Salt Lake has often been commented upon, and the early stages of the maritime species are frequently found locally abundant in both Europe and North America.

More recently Ping ('21) has investigated the occurrence and habits of *Ephydra subopaca* Loew, a common inhabitant of brine pools along the Atlantic seaboard, which he found to be abundant in the saline pools connected with salt works near Ithaca, New York. According to Ping, this species will develop readily in water having a salinity of 9%, or less, but in fresh water the larvæ are utterly unable to undergo their development as he found by attempting to rear them in this medium. The fully grown larvæ and puparia were, on the other hand, able to withstand the effect of fresh water.

The surprising adaptability of the Ephydrid larva is well illustrated by the Californian "petroleum fly," *Psilopa petrolei* Coq. whose larvæ inhabit pools of crude petroleum in large numbers where they probably feed upon flying insects that drop into the oil and are drowned. The habits of this remarkable fly were first described by Howard ('99) and the adult by Coquillett ('99), and the species has more recently been studied by Crawford ('12).

With these facts in mind I fully expected to find the larvæ of Ephydra breeding, perhaps quite commonly, in the thermal waters of Yellowstone Park. Much to my disappointment no larvæ were found during the first two weeks of our stay, but finally in the Norris Geyser Basin one pool yielded some larvæ and puparia, and later in the day they were found again about half a mile further south in the overflow of water running through a sulphurous marsh. In both places the water was only slightly tepid, and filled with a luxuriant growth of a

filamentous alga. Both lots of larvæ were imbedded in the mass of alga from which they were later extricated only after considerable manipulation under the binocular microscope.

This species proves to be a true Ephydra and the adult has been kindly identified for me by E. T. Cresson, Jr., as *E. pectinulata* which he described (Cresson '16) from 40 miles east of Lusk in southeastern Wyoming. A description of the larva and puparium is appended.

Ephydra pectinulata Cresson.

(Fig. **5**.)

Larva. Total length 6 mm.; of anal tube 0.6–0.9 mm.; respiratory tube 0.4–0.6. Body pale yellowish or nearly white, without darker markings except those due to the varying density of the spiny vestiture. Thus in dorsal view there are darker bands where the integument is ridged, transverse dorsally and strongly bent and curved laterally; in lateral view these are strongly sinuous, maintaining in general a more or less vertical direction. Prolegs of about equal size, slightly larger posteriorly, with the last pair very much larger; each with about four strong curved hooks which curve forwards on all except the last leg, where the position is reversed and the spines curve strongly forward. Anal respiratory tubes slightly divergent, not sufficiently extruded in any specimens I have seen to show their basal union.

As in most members of the genus, the larva is entirely pale, without darker markings. The thorn-like body bristles are intensely black and appear to vary in size considerably, but this is due almost entirely to the deeply furrowed integument which causes the bristles to be viewed at different angles when the larva is examined under the microscope.

Puparium. Entire length 8.5–9 mm.; apical part from last proleg to fork 1.7–2.0 mm., prong of respiratory fork 0.6–0.9 mm. Very dark brown, the posterior tubular portion yellow; respiratory fork pale, with black tips. Body densely clothed with very minute black thorn-like bristles, those on the upper surface larger than those below and those on the posterior part of the body coarser, especially on the apical tube. On each of the two segments preceding the tube there is on the dorsal surface a small patch of somewhat larger bristles. First to fourth prolegs small, scarcely elevated, each armed with about four well-developed small hooks surrounded by a few thorns noticeably

larger than those covering the body; fifth and sixth prolegs increasingly much larger but with the hooks no larger; seventh slightly smaller than the sixth; eighth the largest and overhanging the seventh, its hooks curved forwards while those on all the other legs curve backwards. Behind the prolegs near the base of the tube is a small tubercle on each side below the lateral line.

The puparium resembles closely those of other species of the genus described by Aldrich ('12). As will be apparent from the measure-

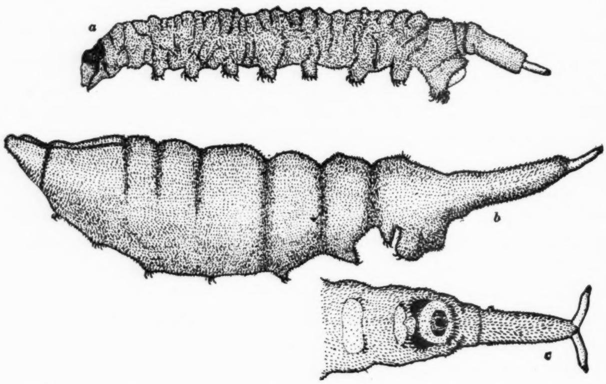

FIGURE 5. *Ephydra pectinulata Cress.* *a*, larva in lateral view; *b*, puparium in lateral view; *c*, posterior part of puparium in ventral view.

ments given above there is little variation in size, except in the length of the respiratory prongs which are extruded much further in some specimens than in others.

I have been able to find only a single reference to the occurrence of any other Ephydridæ in thermal waters. In Japan Matsumara ('15) found a species of Scatella (*S. calida*) in a hot spring.

On account of the long anal tube, these Ephydra larvæ and puparia recall those of the Syrphid fly, Eristalis which occurs also, though rarely, in sea water. Packard ('69b) years ago reported a species of this genus from salt pits and recently Lamb ('11) has reared *E.* (*Lathryophthalmus*) *æneus* Scop. from larvæ found in rock pools on the English coast. Ping ('21) also mentions the occurrence of rat-tailed maggots, which are no doubt a species of Eristalis in artificial salt pools near Ithaca, New York, having a salinity as high as 9%.

Order Coleoptera.

The members of this order occur more generally and abundantly in thermal waters than those of any other group of insects, and moreover, there appear to be some species that are restricted to warm springs and able to thrive at somewhat higher temperatures than those generally suitable for animal life.

Quite naturally a very large part of the references to the Coleoptera of thermal waters relate to the European fauna. In his extensive studies of the animal life in the various Italian hot springs, Issel ('01, '10) lists a considerable series of beetles distributed among four families. These include three species of Dytiscidæ, *Hydroporus tessellatus,* living in water at 30°–35° C., *Bidessus thermalis* (45°) and *Bidessus geminus* (30°–42°); two species of Gyrinidæ *Gyrinus elongatus* (30°–35°) and *G. distinctus* (30°–37°); seven species of Hydrophilidæ belonging to six widely separated genera, *Hydroscapha gyrinoides* (30°–46°), *Helophorus alternans* (39°), *Berosus affinis* (30°–35°), *Helochares dilutus* (39°–40°), *Laccobius gracilis* (35°–40°), *L. gracilis,* var. *sardous* (= *sellæ*) (40°–45°), and *Cœlostoma* (*Cyclonotum*) *hispanicum* (37°–38°); and one Dryopid, *Dryops luridus* (37°–38°). From the hot springs of Fordongianus on Sardinia Krausse ('13) lists one Dytiscid, *Hydroporus pubescens* and a number of Hydrophilids, *Octhebius impressus, O. pusillus, O. nanus, Limnebius evanescens* and *Helochares thermicola* (?). Four other water beetles are listed by Plateau ('72) as occurring in various European hot springs: *Agabus bipustulatus* at Ems (38° C.), *Hydroporus transversalis* at Loèche-les-Bains (39°), *Hydaticus transversalis* at Luxeuil and Ems (39°), and *Hydrous caraboides* at Néris (40°).

From these citations it is evident that a great many palæarctic beetles have taken up their abode in warm springs, some of them apparently being restricted to this habitat (*Laccobius gracilis* (= *sellæ*)), and others, like Hydroscapha, extending their tropical range very considerably by availing themselves of thermal water. It will be noticed also that these two occur at the warmest temperatures, 45°–46° C., several degrees higher than can be endured by unacclimatized animals. Issel ('08) calls attention also to the very sporadic and localized occurrence of these two species.

Similar observations have been made in many localities, and even in India the botanist Hooker, many years ago ('54), found a water-beetle provisionally identified as Colymbetes in water at 44°–45° C. (112° Fahr.) in the hot springs at Soorujkoond in the Behar Hills.

In America Schwarz ('14) has published a rather extensive list of

Coleoptera collected by himself and Mr. H. S. Barber at Hot Springs, Castle Creek Canyon, Arizona, in the pools and small stream containing warm water flowing from the springs. In the warmest water (42°–46° C.; 110°–115° Fahr.) they found two Hydrophilids, *Hydroscapha natans* and *Helochares normatus,* the latter also in cold water near by. Along a streamlet where the water had cooled to about 38° C. (100° Fahr.) eight species were encountered in addition to these: two Dytiscidæ — *Laccophilus pictus* and *Bidessus subtilis;* five Hydrophilidæ — *Helophorus obscurus, Epimetopus thermarum,*[3] *Berosus* sp., *Paracymus ellipsis*[4] and *Chætarthria minor.* In addition, the larva of a Scirtes (?) of the family Helodidæ was present. Of this latter series only one, the Bidessus, was also in the cold water near by, although all except *Paracymus ellipsis* are known from waters of normal temperature. Concerning the latter, Mr. Fall tells me that it is most closely allied to *P. elegans* and *P. lodingi,* the former of which has occurred only in salt or brackish water.

A most interesting fact appears from these observations; that Hydroscapha has taken up its abode in certain hot springs of both hemispheres, and that in both places it inhabits water of unusually high temperature.

According to Sherman ('13), *Deronectes striatellus,* a Dytiscid occurring in the southwestern United States, has been found by Schwarz in water of 40.5 C. (105° Fahr.).

Relating to the coleopterous fauna of the hot springs of Yellowstone Park, there is a very interesting account by Hubbard ('92), published in the form of a letter which contains a number of references to species observed by its writer. These include two Hydrophilidæ, a species of Enochrus (Philhydrus) living in tepid water at Mammoth Hot Springs and an Ochthebius and its larva inhabiting water which is very much warmer. It is probable that the Octhebius was *O. interruptus* and the Enochrus, *E. carinatus.* Hubbard found also two Helmidæ, which he refers to the genus Helmis, one in running tepid water and the other in the Firehole River below the overflow from the Excelsior Geyser at a temperature which he estimated as 21°–24° C. (70°–75° Fahr.). He also refers to several beetles found in the warm soil about the geysers and hot pools—Nebria, Bembidium and several other Carabids (Amara, Pterostichus and Patrobus). None of these appeared however to be peculiar to the warm springs.

[3] Not described till the following year by Schwarz and Barber ('17).

[4] This was listed by Schwarz as *P. subcupreus,* but later described by Fall ('10) as a new species.

My own collections contain six species of aquatic Coleoptera from the thermal waters of Yellowstone Park, three species of Dytiscidæ and three Hydrophilidæ. For their identification I am deeply indebted to Mr. H. S. Barber who kindly examined the collection, as well as to Mr. H. C. Fall who determined two species which were not in the collection of the U. S. National Museum and further gave me a number of interesting notes on other water-beetles which have been incorporated in the present account.

Bath Lake, near the Mammoth Hot Springs, proved to be the most lucrative spot as five species were found there, beneath the fragments of travertine which line the edge of this pond. The most abundant form is *Tropisternus californicus*, a species that has evidently extended its range in this instance. Another smaller Hydrophilid, *Enochrus carinatus*, was obtained in smaller numbers; this is a species characteristic of the Pacific slope, where it has been reported from Oregon to southern California.

Three Dytiscids were taken in Bath Lake also: *Hydroporus humeralis*, a widespread boreal species; *Deronectes griseostratus*, another boreal form; and *Coelambus sellatus*, originally described from the Dakotas. The temperature of Bath Lake is 33° C. (91° Fahr.)

At West Thumb two species of beetles were obtained. In a slightly warm sulphurous pool containing great quantities of a Chara-like plant the same Tropisternus (*T. californicus*) was present in smaller numbers than in Bath Lake. In the running water which forms the overflow from hot springs at this place another small Hydrophilid not seen elsewhere was abundant, hidden beneath the sheets of highly porous travertine under which the water flows. At this point the temperature of the water ranges about 38° C. (100° Fahr.).

Larvæ of one Hydrophilid were numerous both at Bath Lake and West Thumb. These agree closely with the descriptions and figures of species of Tropisternus recently published by Wilson ('23) which, together with their large size, indicates without doubt that they are the larvæ of *Tropisternus californicus*.

In his account of the aquatic invertebrate fauna of Yellowstone Park Forbes ('93) mentions the occurrence of a species of Coelambus in the overflow water that fills a lagoon on the west side of Lewis Lake. This is no doubt the *Coelambus sellatus* mentioned above. At the same place Forbes obtained several Hydrophilid larvæ which appear never to have been identified.

In the case of the Coleoptera inhabiting thermal waters, it is less satisfactory to draw conclusions concerning their relationships to

marine, brackish-water or alkaline-water forms than it is in the orders of insects previously considered. In the first place there seem to be almost no truly marine coleoptera, and the aquatic habit among the larvæ of beetles is restricted to only a few families. In these, however, it occurs almost universally, as for example in the Dytiscidæ, Gyrinidæ, Hydrophilidæ, Dryopidæ and Helmidæ. Nevertheless it is evident that several of the genera mentioned above as inhabitants of thermal waters are represented in the saline and brackish-water fauna. Thus forms of Coelambus and Hydroporus are characteristic of the maritime and submaritime fauna of England (Keys '18), and this is true also of Gyrinus (*e. g. G. marinus*). Similarly, a species of Hydroporus is a characteristic inhabitant of the salt marshes near Odessa on the Black Sea (Butschinsky '00). In America Packard ('73) reported *Laccophilus decipiens* from the saline pools near Great Salt Lake, Utah, and Sherman ('13) mentions six genera of Dytiscidæ that are represented in salt marshes: Coelambus, Coptotomus, Laccophilus, Thermonectes, Agabus and Copelatus, and of these it will be noticed that two, Coelambus and Laccophilus, occur in thermal waters, of which they are, moreover, particularly characteristic. Several names have been given to the Laccophilus which occurs so generally in European hot springs, but according to Issel ('10) all are to be referred to a single species, *L. gracilis* (= *L. subtilis*) and its variety *L. gracilis* var. *sardous*, of which *L. sellæ* and *L. thermarius* are synonyms. Sherman believes that no North American species are restricted to a saline environment. Among the Hydrophilidæ, however, Leng ('13) speaks of *Enochrus* (*Philhydrus*) *hamiltoni* as restricted to salt marshes, and it will be noted that this genus occurs in thermal waters also. Other species that may live in brackish water he believes occur in greater numbers in fresh water. It is of interest to note, however, that Packard ('73) reported *Berosus punctatissimus* from Great Salt Lake and Fall ('01) described *B. salinus*, a salt-water species from Lower California; and that *Berosus affinis* occurs, as noted above, in hot springs in Europe. *Tropisternus salsamentus* (Fall '01) is also a salt-water species, and Mr. Fall tells me that he has taken it together with *Berosus salinus* and *Paracymus elegans* in a small salt lake or pond with a saline content greatly in excess of the ocean itself.

As to the exact concentration of salt which may be endured by Hydrophilid larvæ and adults, Florentin ('99) records Hydrophilus larvæ in water containing 123 grams of salt per litre and *Acanthoberosus spinosus* in water containing 100 grams per litre.

Order Trichoptera.

Caddis-fly larvæ also occur in the sulphurous ponds, although not so abundantly as in the clear cool water of the mountain streams. In one large pool on the south side of the road to Soda Butte, about one mile east of Tower Falls, the cases of four species were taken in numbers, deserted however, as the larvæ had already completed their transformations. From a comparison of the cases (Pl. 1, figs. 3, 4, 5) with the figures in Lloyd's recent paper on caddis-fly larvæ ('21), it seems quite probable that all may be referred to the family Limnophilidæ.

The first published reference to the occurrence of Trichopterous larvæ in any of the thermal waters or sulphurous pools of Yellowstone Park is contained in Peale's account ('83) which forms a part of Hayden's geological report for 1882. There he notes the discovery of larvæ of a species of Helicopsyche by Mr. W. R. Taggart in water having a temperature of 42° C. (108° Fahr.). Forbes ('93) refers to the occurrence of trichopteran larvæ ("case-worms") in a warm spring near the western side of Lewis Lake at 65° C. (150° Fahr.) but undoubtedly the larvæ were in a cooler part of the pool. Helicopsyche has never been reported from such waters in other parts of the world, nor is it ever found in salt or brackish water.

In Europe Perty ('41) found larvæ of an undetermined Phryganeid in the hot springs of Lenk, Switzerland. The temperature was not recorded, but the maximum in these waters is 51° C. (123° Fahr.)

One member of the order Trichoptera lives in tidal waters in Europe. This is *Agrypnetes crassicornis* McLachl. According to Rousseau ('21) the larvæ of this insect are met with mainly on the seashore in brackish water, where they live among Fucus and other marine algæ, although they are able to develop equally well in fresh water. In Great Britain Parke ('63) found the larvæ of *Limnephilus pellucidus* living in brackish water. Miall ('95) refers to observations of the Rev. A. E. Eaton who found an abundance of small Hydroptilidæ developing in salt or brackish water near the borders of the African Sahara. Even in New Zealand McLachlan describes the habits of a caddis-worm which occurs between the tide marks, where it utilizes bits of coralline seaweed for the construction of its case, behavior which at once stamps it as a truly marine insect.

Order Odonata.

The occurrence of nymphs of Odonata in brackish water is well known and their behavior in water of different salinities has been

examined experimentally by Osburn ('06). He found the nymphs of various species in brackish water on both the northern Pacific coast of America and in New England, but found none restricted to the salt marshes. Similar habits have been observed among European species, Indian ones (Annandale '07) and in Australia by Tillyard ('17). Osburn determined that a density of about 1.01 (less than half that of sea water) did not prevent the hatching of the eggs of several species, nor the development of the nymphs, but that they were unable to develop in water of greater salinity. One record of a nymph of a Libellula in Europe is given by Florentin ('99), who found it in water containing 18 grams of salt per litre.

In alkaline or sulphurous waters fewer observations have been made, but Schwarz ('91) records the presence of dragon-fly nymphs in the salt flats bordering Great Salt Lake, Utah, living in brackish and sulphurous water. These are possibly the Argia referred to in the next paragraph. In a highly alkaline lake at Roswell, New Mexico, and also in a strongly alkaline stream in the Arroyo Pecos, near Las Vegas in the same state, Needham and Cockerell ('03) report the presence of nymphs of several species.

In thermal waters Odonata do not appear to occur very generally, although there are a number of cases on record. As some of these show quite clearly how the opportunity to breed in warm water has extended the range of tropical or subtropical forms, I have been tempted to refer to them in detail. Cockerell found nymphs of the Agrionid *Hyponeura lugens* Selys present in the Gallinas River at Las Vegas, New Mexico, at a point where the water is perceptibly warmed by the addition of water entering from the hot springs at that place (Needham and Cockerell '03). This species belongs to the upper Sonoran fauna and Las Vegas is in the Transition Zone. At the same place Cockerell obtained nymphs of an undetermined species of Argia which was later figured by Needham ('04), who records its occurrence also in White Sulphur Springs near Great Salt Lake, Utah, and in Yellowstone Park. Possibly the nymphs from the Yellowstone were living in warm water there also. Needham (*loc. cit.*) records *Libellula saturata* Uhler, a Sonoran species, from Yellowstone on the basis of nymphs obtained there, presumably in warm water, by S. A. Forbes, and an adult taken by O. S. Westcott. These nymphs are possibly the "libellulid larvæ" mentioned by Forbes ('93) which he found in a lagoon filled with the overflow waters of a geyser at the western side of Lewis Lake. This locality is the northernmost record for the species.

The occurrence of unidentified Odonate nymphs in hot springs in California has been reported by Kellicott ('97). The nymphs were obtained in a pool in Lassen County, California, said to be near the boiling point at one end and of blood heat at the other, the insects occurring in the warmer parts of the pool as well as at the cooler end. His figures show them to be of the broad libelluloid type.

In the slightly warm alkaline thermal waters, probably about 75° Fahr., of Lake Huacachina in Peru, Tamayo and Garcia ('06) have reported the occurrence of Libellulid nymphs in large numbers.

Order Plectoptera.

The nymphs of an undetermined may-fly have been recorded from Yellowstone Park by Forbes ('93). They were collected in a warm spring near the west shore of Lewis Lake, at a temperature said to have been 66° C. (150° Fahr.), although it would seem almost certain that this is an error and that the temperature must have been considerably lower.

In Europe the nymphs of one species, *Chloë diptera,* have been found living in the hot springs of Luxeuil in water of 45° C. (113° Fahr.) according to Plateau ('72). This is an unusually high temperature for an insect.

Order Hemiptera.

The only Hemiptera collected were numerous specimens, both nymphs and adults, of *Ambrysus heidemanni* Montandon. These were kindly identified for me by Professor H. M. Parshley. The bugs were in warm running water (96° Fahr.) in the overflow from Firehole Lake. This water is very heavily charged with silica, which is deposited in a thick layer on all objects in the stream. This species was originally collected in thermal water in Yellowstone Park and as it does not appear to have been taken elsewhere is probably a member of the true thermal fauna.

Members of another family *Corixa hieriglyphica* Duf. have been found in thermal waters in Europe. Issel ('00) found this species living in water at 40° C. In Yellowstone Park Hubbard ('92) saw an unidentified Corixa in a small tepid stream which was depositing silica rapidly upon submerged objects, and Forbes ('93) found a member of the same genus in the warm overflow waters of a geyser that form a lagoon on the west side of Lewis Lake. The European *Notonecta glauca* is said by Plateau ('72) to occur at Vichy in eastern France in water at 19°–45° C. (57°–113° Fahr.) in company with *Nepa cinerea.*

ARACHNIDA.

A few specimens of an undetermined species of Pirata were obtained in the porous siliceous crust over running warm water in the overflow from boiling springs at West Thumb. Dr. R. V. Chamberlin tells me that he has observed certain species of this genus associated with other hot springs in the western United States.

Spiders have been reported several times at least as associated with hot springs. One said to be a Lycosa, but quite possibly also a Pirata, occurs about the boiling pools at Hammam Meskoutine in Algeria where Gervais ('49) observed them running about over the hot soil and even venturing onto the surface of the hot water in small craters. The occurrence of spiders was also noted years ago on the hot soil about a thermal spring in Owen's Valley, California, by Wood ('68).

Another Arachnid, the mite, *Hydrachna cruenta*, has been found according to Plateau ('72) at Luxeuil in water of 46° C. (115° Fahr.), an unusually high temperature for an Arthropod.

CRUSTACEA.

No special search was made for Crustaceans in the thermal waters of the Park and any extremely minute forms which may exist there were not collected. One species of Amphipoda was, however, so abundant in several places that numerous specimens were preserved. This proves to be *Gammarus limnæus* Smith, a widespread form, whose distribution is so interesting that I have been led to consider it in the present account.

It was described by Smith ('75) from material collected by the naturalists accompanying the Hayden exploration party in a cool spring in the Firehole Basin, Yellowstone Park, and in a lake near Long's Peak, Colorado. Smith described also from the Wasatch Mountains, Utah, *Gammarus robustus*, now regarded as a synonym of *G. limnæus*. It was later reported as *robustus* by Forbes as present about Lewis Lake, in a warm lagoon on the west shore and in a spring near by. The temperature of the water in the latter is given as 150° Fahr., but this is evidently in error. My specimens agree perfectly with the description and figures given by Weckel ('07) who records the species also from localities in Maine, Michigan, Wisconsin, New Mexico, Idaho, Utah and Montana. Later, Pearse ('14) found it in material from northeastern Nevada at elevations of about 5,000 feet,

and Shoemaker ('20) found it well represented in the collections of the Canadian Arctic expedition made in Alaska and the Canadian northwest territories. In one case specimens were secured on June 23 under two metres of ice in an inland lake near Bernard Harbour, and in another from "Warm Creek" near Camden, Alaska. Whether this creek actually contains warm water is not stated, but in his report on the algæ Lowe ('23) says that this creek comes from some warm springs further inland, and that it contains calcareous sinter with imbedded algæ.

The present specimens were collected in the swiftly running overflow from boiling springs at West Thumb and in the outlet to Firehole Lake where the water had cooled to about 100° Fahr., as well as in a sulphurous pond east of Tower Falls, where they were especially abundant.

This species occurs therefore not only across the entire northern part of North America, but thrives beneath the ice as well as in warm water. It is one of a number of fresh-water species of the genus which includes also typical marine forms. In view of the classical case of the Phyllopod Crustacean, Artemia, and other no less interesting experiments on other genera of this group of animals (Cyclops, Daphnia, *et al.*) made by Schmankewitsch ('72, '75, '77), subsequently substantiated in additional forms of Artemia in other parts of the world (v. Günther '99 and Kellogg '06) where certain morphological differences depend upon the salinity of the water,[5] it is natural to inquire whether such variations occur in a species like the Gammarus here considered. So far as I can ascertain such variations do not exist, at least in relation to habitat. Smith did erect two species to include the present *G. limnæus* but his forms *robustus* and *limnæus*, although differing in slight details, appear to bear no relation to habitat. Certainly my specimens do not approach in any way related species, *e. g. G. pribilofensis* Pearse.

We do find, however, as with most of the groups of insects, where those including marine species have also forms adpated to life in alkaline or thermal waters, that the genus Gammarus is no exception. Observations have been made showing the ability of a fresh-water species to withstand saline water. Chevreux and Guerne ('92) found *Gammarus rhipidiophorus* Costa living in pools close to the shore of the Mediterranean where the water becomes brackish during the

5 Günther (*loc. cit.*) states that the morphological characteristics of Artemia are so closely correlated with the density of the water that they furnish a determination of the salinity with an error of less than .03 in specific gravity.

summer, due to a temporary connection with the sea. *Cyclops bicuspidatus* Claus, a fresh-water copepod of Europe, also occurs in salt pools and in this species Florentin ('99) states that those in brackish water actually acquire varietal differences like the forms studied by Schmankewitsch. This genus is also represented in thermal waters (Pavesi '81).

Gammarus locusta of Europe occurs similarly in thermal waters, and has been found in the warm waters that discharge from the hot springs at Abano in northern Italy (Martens '24) and *G. roeselii* is known from two localities in hot springs (Plateau '72), Piemont at 34.4° C. and Gastein at 36° C.

Another Amphipod, *Hyalella knickerbockeri* Bate, has been reported from Yellowstone Park. This is the *Allorchestes dentatus* discovered by Forbes ('93) in thermal water at two stations near the west shore of Lewis Lake. He found this species in a lagoon which is filled with the overflow waters from a geyser and also in a warm spring. The temperature of the latter is given as 65° C. (150° Fahr.), but this certainly cannot refer to the part of the pool in which the crustaceans were living. This species enjoys a very wide distribution across North America from Maine to California and extends into the American tropics. It varies considerably and has received several names (*Hyalella dentata* Smith ('75), *Hyalella inermis* Smith ('75), and *Hyalella faxoni* Stebbing ('03)) since it was originally described by Bate ('62), but Weckel ('07) considers the several forms under one name. From a search of the literature I have been unable to find any association between habitat and the several variations, although it is quite possible that some such correlation exists. Professor T. D. A. Cockerell writes me that he collected this species in hot water at Las Vegas Hot Springs, New Mexico, so that it is undoubtedly a common inhabitant of thermal waters.

Cypris balnearia Moniez occurs in the well-known Algerian thermal waters at Hammam-Meskhoutine, where Moniez ('93) found this species so abundant in water at 45°–50.5° C. that it formed a sort of continuous chocolate-colored zone along the edge of the water. An undetermined Cypris was found there previously by Gervais ('48) in water at 40° C., probably the same species, although Moniez does not mention it, having probably overlooked Gervais' short note. At Ischia in Italy, Pavesi ('81) observed *Cypris thermalis* Costa already known by its describer to be an inhabitant of hot springs. Another member of the genus, *C. fuscata*, enters the thermal fauna at Néris (34.4° C.) and in the Hungarian springs at Gastein (36° C.). Gervais (*loc. cit.*) also reports the European fresh-water crab, *Telphusa fluviatilis*,

at Hammam-Meskhoutine in the overflow water having a temperature of 36°–40° C., and Studer ('89) reported a Papuan crab of the genus Ocypoda on the coast of New Guinea in water heated to 50° C. by hot springs that discharge into the sea.

Even Isopod crustaceans have been found in thermal waters, perhaps not so surprising in an essentially marine group of highly adaptive animals that have developed fresh-water, terrestrial and parasitic forms. Thus in the family Sphæromidæ, typically marine, there are a number of fresh-water species and two that have been found so far only in thermal waters. They are *Exosphæroma dugesi* Dollfus ('93) from Aguascalientes, Mexico, and *E. thermophilum* Richardson ('97, '04, '05), collected by Cockerell in a warm spring near Socorro, New Mexico. The palæarctic *Sphæroma rugicanda* Leach occurs in brackish water and two species of Cæcophæroma (*C. virei* Dollfus and *C. burgundum*) inhabit the waters of the Grottos of the Jura.

Many years ago Woodward ('79) described two fossil species of Eosphæroma from the Gurnet Bay deposits in England. These beds, as noted elsewhere in the present paper, were undoubtedly laid down in connection with hot springs and the finding of these species shows that the occurrence of Sphæromidæ in thermal waters dates back at least as far as the Oligocene.

The common fresh-water *Asellus aquaticus* of Europe is sometimes found in hot springs. Plateau ('72) records it from Loèche-les-Bains in water at 42.5° C. (108.5 Fahr.).

The same author records the small copepod, *Cyclops quadricornis*, from Néris and Gastein in water at 34.4° C. and 36° respectively.

Ziegelmayer ('24) reports the occurrence of *Cyclops serrulatus* or a closely related species in the sulphur springs, Aque Albule, in Italy at a temperature of 21°–23° C. (70°–73° Fahr.). By analysis this water appeared to be entirely devoid of dissolved oxygen and thus presents a similar condition to that referred to in connection with the blood-worms of the genus Chironomus mentioned on a previous page, except that in this case the Cyclops possesses no hæmoglobin which might aid it in utilizing such minute quantities of oxygen as may exist in this water. Ziegelmayer found these crustaceans covered with tufts of filaments of sulphur bacteria which are attached to certain parts of the body where a pitted structure of the chitinous cuticula affords them a foothold, and he would interpret the association as a symbiotic one.

MOLLUSCA.

Molluscs do not appear to be so abundant in the thermal waters of Yellowstone Park as might be expected, to judge from the considerable variety that has been reported from European thermal springs. Those which I obtained are snails belonging to three genera, Physa, Limnæa and Amnicola. Previously Forbes ('93) has reported "a small Physa" in the overflow water from a geyser at the western shore of Lewis Lake.

In the small stream which forms the outlet to Firehole Lake there were large numbers of a small snail which Dr. H. A. Pilsbry has kindly identified as a dwarf form of *Physa heterostropha* Say. They were in company with the larvæ of Tabanus, the water-bug Ambrysus and the Crustacean, Gammarus, discussed in another part of the present account. This water was at a temperature of 96° Fahr., and is so heavily charged with silica that all objects in the water become coated with a thick blackish coating of this mineral. This dwarf form is, according to Dr. Pilsbry, the one described by Lea ('39) as *Physa aurea* from a hot spring in Bath County, Virginia. Later Binney ('65) suspected this to be a form of the common *P. heterostropha* and quotes Lea's account of its habitat, which is so striking that I have been tempted to transcribe it again: "Mr. Nicklin informed me that he found the *Physa aurea* in a little water course by which a hot and a cold spring discharge their mingled waters. The former exhibits a temperature of 106° and the latter of about 56° of the scale of Fahrenheit. Near the meeting of the waters, one side of the little stream is cold and the other side hot; and multitudes of these beautiful Physæ are to be found on both sides of the line of junction, availing themselves of the power which the locality affords them of changing their climate according to their fancy." *Physa heterostropha* var. *elliptica* has been recorded by Call (*teste* Stearns '01) in Warm Spring Lake, near Salt Lake City, Utah, and the variety *gyrina* from Hot Springs, Panamint Co., California (Stearns '01). In connection with these forms and others referred to in his paper, Stearns found no indication of any dwarfing of the individuals living in thermal waters, although he believes that depauperation is association with brackish water. Still another Physa (*P. heterostropha* subsp. *cupreonitens*) has been described by Cockerell ('89) from hot springs at Wellsville, Colorado ~~Arkansas~~.

Aside from the above, there are references to the occurrence of Physas in European thermal waters. Dubalen ('73) found *Physa*

acuta Drap. in the warm springs of Dax in southern France at temperatures ranging from 88°–91° Fahr., but Issel ('01) does not include the genus in his rather extensive list of molluscs inhabiting the Italian warm springs. A variety of *P. acuta* is mentioned by De Varigny from thermal water at 77°–86 Fahr. near La Preste in the eastern Pyrenees and a form of this species was reported by Dupuy ('77) and Fischer ('81) at Barbotan in southern France at 86° Fahr. This variety is no doubt *Physa acuta thermalis* Dupuy known together with *P. acuta gibbosa* Massot and *P. ataxiaca* Fagot to occur in the Pyrenees only in thermal waters (Gineste '85), where they invade water up to 27°–30° C. *P. acuta* is also recorded from artesian water at Rochefort at a temperature of 32.5°–33° C. (Regelsperger '83, '85).

It is possible that an old reference to a strongly ribbed Physa (*P. costata* Newc.) in Clear Lake, California, by Newcomb ('63, *v.* also Stearns '01), may refer to a species in a near-by alkaline pond (Borax Lake) as there has been considerable confusion in the past concerning the provenience of material from these two lakes, one of which is fresh; the strongly costate shell suggests brackish or alkaline water. In the palaearctic region *Physa fontinalis* occurs in brackish water (Parke '63) and *P. acuta* in salty pools (Coutagne '82).

Lymnæa palustris Müller (identified by Dr. H. A. Pilsbry) was found in large numbers in a warm sulphurous pool formed by the overflow from a hot spring near Mary's Bay, close to the northern shore of Yellowstone Lake. The snails did not extend into the warmer part of the stream where the tadpoles mentioned on another page were found, but were numerous in water of between 80° and 96° Fahr. which contains large quantities of filamentous green algæ. This widespread holarctic species is reported by Issel ('01) from thermal waters in Italy at a temperature of 61° Fahr.

Another species of Lymnæa, unfortunately not represented by any mature individuals, was taken in warm flowing water in the Yellowstone Canyon, near the level of the river and not far below the lower falls.

Issel ('01, '06) found *Lymnæa peregra* and *L. truncatula*, which is probably only a variety of the former, in water ranging from 77°–90° Fahr. (*truncatula*) and at 72.5° (*peregra*) in Italy. *L. peregra* is a common inhabitant of thermal springs in other parts of Europe, occurring in the springs at Barbotan at 86° (Fischer '87) and 88° (Dupuy '77), at Aix at 45° C. (Gineste '85), at Baden at 46° C. (Martens), at Bagnaralo at 37°–38° C. (Issel '06) and in Staffordshire in England at 36.7° C. (Masefield '96). The varieties *truncatula* and *geisericola* are

known from the sulphurous thermal waters of Iceland at 43° C. (Mörch '68, Sikes '13). *Lymnæa vulgaris* occurs in abundance in thermal waters near Lyon according to Locard, and De Varigny records the same species in a creek arising from these springs in water at 77° Fahr. but the individuals were about half the usual size, thus exhibiting the dwarfing noticed elsewhere among many of the molluscs that inhabit thermal waters. This is probably due to some extent to the greater amount of dissolved salts, since fresh-water molluscs which occur in brackish water are generally dwarfed (De Folin '79, Pelseneer '20, Stearns '01). According to Gineste ('85), in the Pyrenees *Lymnæa thermalis* requires warm water, while *L. peregra* is indifferent in this respect. He did not find the former in water above 27°, however, which is far below the temperature at which *peregra* occurs. *Lymnæa peregra* occurs even in very cold water, as its variety *glacialis* is an inhabitant of cold mountain springs. It is also rather widely distributed in brackish and salt pools such as the salt marshes of the Baltic (Pelseneer '20), in the Berre salt pool near Marseille (Gourret '97), in brackish ponds along the Aral Sea (Pelseneer '20), and in the north of England (Cooper '10). In America Dall ('19) found *Lymnæa caperata* Say in the collections made by Mr. Fritz Johansen in northern Alaska. These specimens came from Hot Spring Creek, tributary to the Sadlerochit River, 25 miles inland from Camden Bay on the Arctic coast. This is true thermal water, but the temperature is not indicated.

Amnicola is represented in the sulphurous pools of Yellowstone Park, as a somewhat imperfect shell of a member of this genus forms a part of a caddis-worm case (see Pl. 1, fig. 3) which I obtained in a highly sulphurous pond near Junction Butte, a short distance east of Tower Falls. A species of this genus has been reported from Hot Springs, Bath Co., Virginia (Gould '45), which is possibly *Bithynella nickliniana* Lea (*Paludina* Lea; *Amnicola* Haldeman) (Binney '65b).

The common *Paludina* (*Vivipara*) *muriatica* Lam. of southern Europe occurs generally in fresh water and is known from thermal waters. Linnæus applied the name of *Turbo thermalis* to a species common in hot springs, *Bythinella thermalis*, now known (Issel '06) to occur in water up to 46° C.

In addition to the above, Issel ('01) records the following molluscs from hot springs in Italy: *Melanopsis etrusca* (22°–41° C.), *Theodoxia prevostiana* (32° C.), *T. fluviatilis* (16°–26° C.), *Bythinia tentaculata* (25° C.), *Bythinella etrusca* (25° C.), *Planorbis lævis* (?) (25° C.), *Valvata piscinalis* (16° C.), *Ancylus lacustris* (25° C.).

Among the Pelecypoda, representatives of two genera have been found in thermal waters in Europe, *Pisidium cazertanum*, var. *thermale* by De Varigny at Evaux (24° C.) and by Dupuy ('77) at Cauterets (39° C.). *Unio requieni* has been reported at Barbotan by Dupuy ('77) in water at 31° C. In America Forbes ('93) mentions the occurrence of an undetermined Pisidium in a warm spring near the west shore of Lewis Lake. These are said to have been in water at 150° Fahr. (65° C.) but this must be a mistake.

From the foregoing it will be seen that very high temperatures have been reported for some European molluscs. De Varigny ('93) mentions the occurrence of *Bythinella thermalis* at 37.7° C., but Issel reported the exceptional occurrence of the same species at 46° and its regular appearance at 42° C. Fischer ('87) believed that 42° was the upper limit for molluscs, based on the presence of a species of Hydrobia in the Algerian springs near Bône. This agrees closely with Issel's findings and with observations on American species. Only one apparently authentic record greatly exceeds these. Studer ('90) observed *Neritina thermophila* in New Britain in water at 52° C., a record accepted without comment by Pelseneer ('20). Studer also reported *Ostrea cucullata* growing in brackish water at the same place, heated to 45° C. by water from hot springs that flows into the ocean

FISHES.

The present writer made no observations on the occurrence of fish in the thermal waters of Yellowstone Park, but Jordan ('89) mentioned three species in his report on the fishes of Yellowstone Park. He found the chub (*Leuciscus atrarius*) in the warm water of Witch Creek at 85° (29° C.) and the sucker (*Catostomus griseus*) in the Gardiner River below the mouth of Hot River, at Mammoth Hot Springs where the water reached a temperature of 88° Fahr. (31° C.). He also found young trout in water of 75° Fahr. (24° C.). Exactly similar observations are reported by Doflein ('14), apparently quoted from Jordan's paper.

The many records of fish in thermal waters in Europe, Africa and other parts of the world indicate that their tolerance extends to about 40° C. (104° Fahr.). Thus Gervais ('49) found barbels (*Barbus setivimensis*) in water of 36°–40° C. in the outlet to the Hammam Meskoutine springs in Algeria. Desfountaines (De Varigny '93) found *Sparus desfountainesii* in the hot springs at Cafsa at 38° C.

Rochet d'Héricourt found in hot saline springs in Eritrea small fish at 44° C. Several observers in Ceylon have observed fish in the thermal waters which occur there. The temperature of the pools in which these fish were living did not exceed 32° or 33° C.

In Europe Hoppe-Seyler ('75) made careful observations near Battaglia in the Euganean Hills west of Venice and found fish living in a stream having a temperature of 44°–45° C. at the surface, but with cooler water at lower depths (25°). Here the fish remained in the cooler lower strata and occasionally individuals that came to the surface at too hot a place were overcome by heat rigor from which they did not always recover. Similarly, Knauthe ('95) found experimentally that the death temperature for a series of fishes ranged from 23°–37° C.

It would appear, therefore, for fish that the critical point of heat endurance lies about 40° C. (104° Fahr.). Observations attributing greatly higher temperatures to the medium in which they occur are obviously due to erroneous notes or faulty transcription, as for example the oft-quoted account of Sonnerat (1776), who gives a lengthy and highly embellished account of fish living in hot springs in the Philippines at 86° C.

So far as permanent existence and reproduction are concerned, it seems probable that thermophilous fish live only in waters not exceeding 25° or 30° C.; the lower figure is the one set by De Varigny ('93), and agrees quite closely with observations in Italy by Issel ('01), who found *Leuciscus aula* Bonap. and several other species (Blennius, Anguilla,[6] Squalius, Telestes) in water at from 25°–26° C. (77°–79° Fahr.). Experiments by Maurel and Lagriffe ('99) showed that some species may live at 30°–32°, but that ordinarily above 25 degrees respiratory disturbances set in, usually passing into a "delirium" at 30° C.

AMPHIBIA.

Large numbers of tadpoles were observed in one locality near the north shore of Yellowstone lake in a very slowly moving stream that has its origin in a hot sulphurous spring. This little stream is very hot at its source, but after a distance of perhaps a hundred feet it

[6] An old mention of "anguilles" in the thermal waters at Aix by Saussure (1796) evidently does not refer to eels, although it has often thus been quoted. At that early date Saussure had evidently taken great pains to search for living things and speaks of "des rotifères, des anguilles et d'autres animaux des infusions" in these waters.

gradually broadens out, becomes stagnant and cools rapidly. The coolest parts (50°–70° Fahr.) are well stocked with masses of green filamentous algæ and contained many tadpoles. Further up the stream where the water was warmer, their numbers diminished, but numerous individuals were actively swimming about where the temperature of the water ranged between 104° and 106° Fahr. They did not, however, appear to enter the warmer water farther up stream, although adult frogs frequented the thick vegetation along the sides where the water was still warmer. A number which I attempted to catch in my insect net escaped and appeared to enter the water or soft mud, although observation was difficult on account of the presence of steam vents here and there near the edge.

Dr. Thomas Barbour has kindly examined the tadpoles and assures me that they undoubtedly belong to the genus Rana, and that they are quite probably *Rana temporaria pretiosa* Baird and Girard. This species has been reported from Yellowstone Park by Cope ('89) on the basis of specimens collected by Merriam in the Upper Firehole Basin, and Cope (*loc. cit.*) believes that the *Rana septentrionalis* mentioned by him ('72) may be the same form. It was from Carrinton's Lake.

Of special interest in connection with these tadpoles are some experiments made a number of years ago by Davenport and Castle ('96) on tadpoles of the common toad of the eastern United States, *Bufo lentiginosus*.

They found that tadpoles reared in water at an ordinary temperature of about 60° Fahr. (15° C.) were unable to withstand temperatures approximating 104° Fahr. (40° C.) as they passed into heat rigor at about that point (from 39.5° to 41° C.). They then reared the tadpoles from the egg at somewhat higher temperatures, 76° Fahr. for a time (three or four weeks), followed by a temperature of about 92° Fahr. for a varying period of five days to three weeks. After this treatment the tadpoles showed a markedly increased ability to withstand heat and went into heat rigor at from 106°–111° Fahr.

It is evident therefore that the tadpoles from the thermal waters of the Park were living in water at practically the lethal temperature for unacclimatized toad tadpoles, and only a few degrees below that which proved fatal for those acclimatized by prolonged exposure to abnormally high temperatures. There is every reason to suppose that the heat reactions of frog and toad tadpoles differ in no essential way. This is also borne out by experiments made by Maurel and Lagriffe ('00), who found that frogs could not withstand a water temperature above 36°–38° C. There is, as a matter of fact, probably

only a slight range of temperature at the higher end of the scale over which these amphibians might become acclimatized, since Vernon ('99) has shown experimentally that the heat rigor is due to an actual physiological state of the muscular tissue. This rigor he obtained in frog and toad muscle at between 38° and 40° C.

Davenport and Castle (*loc. cit.*) cite an old statement, made by Spallanzani in 1777, to the effect that he had observed frogs in thermal water of 46° C. (115° Fahr.), but the accuracy of this is very doubtful. Nevertheless more recent observers have noted batrachians in the thermal waters of the Old World. Gervais ('48) collected adults and tadpoles of *Rana esculenta* Linn. in the overflow from the springs at Hammam-Meskhoutine, in Algeria, at from 36°–40° C. Issel ('01) obtained the same frog from several Italian springs at temperatures ranging from 25° to 40° C., and mentions a toad, *Bufo viridis* Laur., from one spring at 25° C. Hooker ('54) found frogs at the Sooruj-koond hot springs, in India, in water at 32° C. (90° Fahr.).

Tadpoles are, of course, like other amphibians, unable to live in sea water, although it has been shown that they may be gradually accustomed to a very considerable salinity. Thus Yung ('85) was able to bring them into water containing 10 grams of salt per litre without ill effects. That tadpoles may actually develop in brackish water in nature is attested by a statement by Schwartz ('95). In speaking of the saline pools in the flats near the shore of Great Salt Lake, Utah, he says: "Here in the midst of the pools covered with the Ephydras, a commotion was occasionally observed as if a fish of considerable size had risen to the surface of the water. Mr. Hubbard succeeded in capturing one of these mysterious creatures, which proved to be the larva of a toad. It appeared that this tadpole comes to the surface of the water right among the Ephydras, with the dexterous motion of its tail sweeps a goodly number of flies into its wide mouth, and retires again to the bottom of its ill-smelling abode." Coming from two such accurate observers as Schwarz and Hubbard there can be no doubt that tadpoles inhabit these pools, but unfortunately no statement is made as to the probable amount of salt in the particular pools, and the supposition that they are toad tadpoles is probably a mistake as toads transform into adults when very small whereas the larvæ of our common frogs attain much greater size before transformation.

European observers have occasionally found a similar association of palæarctic batrachians with brackish water. Thus Florentin ('99) found tadpoles in water containing 8 grams of salt to the litre and

Boulenger ('97) speaks of the common *Rana esculenta* occurring in water of somewhat higher density (11 grams per litre). He mentions also (Boulenger '99) a young specimen of *Hyla arborea,* collected in salt water by Günther, at Lake Urmi in northwestern Persia. Dr. Thomas Barbour tells me that *Rana virescens sphenocephala* Cope of the southeastern United States lives occasionally in slightly brackish water, although he doubts whether the tadpoles could develop in this medium. Experimental attempts to hatch the eggs of frogs in weak salt water accord with this, as Hertwig ('97) found a concentration of 7 grams of salt per litre soon arrested their development.

INSECTS IN A STEAM VENT.

Scattered over the ground in various parts of the Park, especially where boiling pools or geysers occur, are numerous openings in the soil. Some of these are quite cool, others warm or hot, and from some steam escapes. The cavities into which they lead may in the case of those having a low temperature contain such large quantities of carbon dioxide that small mammals are sometimes overcome and suffocated; the warmer ones emit malodorous gases, probably consisting in great part of hydrogen sulphide, with perhaps the addition of some sulphur dioxide. Those which are actually steaming usually have an unpleasant odor and frequently there is such a copious escape of steam that it is dangerous to attempt to insert the hand or to place the face too close to the opening. In a small one of these extremely hot cavities near Firehole Lake we were surprised to see the ground just inside the opening covered with a mass of insects which had been killed by the heat. By means of a stick we succeeded in extricating a handful of these from the accumulation which appeared to contain a quart or more, and were able to get an idea of what it was composed. The majority were blow-flies (Calliphora), with a number of another smaller blue-green Muscid, but there were numerous insects of other kinds, including two species of wasps (Tachytes and Bembex), a bee, a Hesperiid butterfly, two species of Tipulidæ and a Cerambycid beetle. What had attracted this miscellaneous assemblage is difficult to surmise. The fetid odor may have served as a lure to the blow-flies, and the wasps which store their nests with such flies may have come in pursuit of the latter, but the crane-flies, bees and longicorn beetles could hardly find more than warmth to attract them; once enveloped in the steam, escape is of course impossible.

We noticed many other instances of insects floating on the surface or drifting about in the water of the boiling pools. Many are caught thus and of course instantly killed by contact with the extremely hot water. Like sticks, leaves and other objects in these pools, the insects soon begin to accumulate deposits of calcium carbonate or silica on the surface of the body and sink to the bottom to aid in the formation of the deposits of travertine and sinter. In the calcareous springs the mineral matter forms in irregular granules or flocculent masses and such organic inclusions are not actually fossilized in the true sense. The accompanying photograph (Pl. 1, figs. 1, 2) of a caterpillar taken from a calcareous hot spring shows clearly the process of incrustation.

A published reference to a similar occurrence of dead insects in fumaroles is contained in Moseley's account of the Challenger expedition ('79). He found on the slopes of the volcano on Banta Island large numbers of flying insects dead in the cracks in the hot soil, killed, as he says, by the poisonous volcanic vapors. As these observations were made near the top of the mountain, the number of insects caught was undoubtedly augmented by the abundance of flying species, which he noticed, in conformity with the usual tendency for insects to fly in great numbers to the tops of mountain peaks.

The great numbers of dead insects in the boiling pools of Yellowstone Park has been commented upon by Hubbard ('92) and by Schwartz in the official minutes of the meeting of the entomological club of the American Association for the Advancement of Science for 1891 (Canadian Entom., vol. 23, p. 230).

Postscript

While this paper was in press Böving (Bull. U. S. Dept. Agric. No. 1218, p. 13. (1924)) has published a description of the larva of *Tabanus punctifer* and it appears that I was correct in the surmise that the larva described on page 399 belongs to this species. Unfortunately Böving does not mention the taxonomic characters used by Hart in describing the larva of Tabanus, but there seems to be no question as to the identity of the two series.

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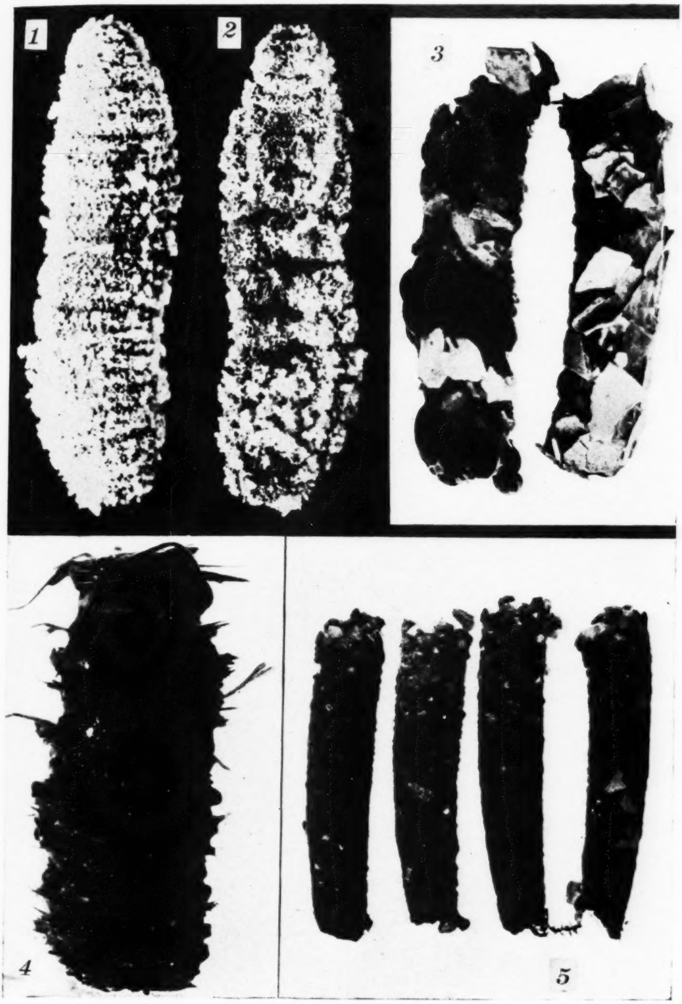
EXPLANATION OF PLATE.

FIGURES 1 and 2. Two views of caterpillar drowned in hot calcareous pool, showing manner in which immersed objects become encrusted with calcium carbonate.

FIGURES 3, 4 and 5. Cases of three species of caddis-worms from sulphurous pond. One of those in Figure 3 has a minute shell (Amnicola) attached.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